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Miscellanea

Geology Vol 44 No 1 30 June 1988

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Palaeocene wood from the Republic of Mali

M. Crawley

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Synopsis

A new species of fossil Leguminosae, ?*Caesalpinioxylon moragjonesiae*, is described from the Tertiary deposits of the Tilemsi valley area, Republic of Mali. Anatomical comparison is made with Recent and fossil woods. Silicified vestured pits are illustrated for the first time using the scanning electron microscope. It is suggested that more studies of such pits would assist in classification of fossil dicotyledonous wood.

Introduction

In 1981 a joint British Museum (Natural History)/Kingston Polytechnic expedition visited the Tilemsi valley area of Mali, west Africa. At Samit, specimens of fossil wood were collected from strata of Middle to Upper Palaeocene age (Krasheninnikov & Trofimov 1969; R. T. Moody, personal communication). The object of this paper is to describe the structure of the petrified wood, which represents a new species of fossil Leguminosae. Particular emphasis is placed on study of the vestured vessel pitting.

Material and methods of study

The three pieces of wood are silicified, the largest measuring some 18 cm by 8 cm. Thin sections were prepared in standard orientations for observation by optical microscopy. Study of the pitting was also made by scanning electron microscopy (SEM), using fractured chips of the wood (Beck *et al.* 1982). The average density of vessels per unit area was determined by counting as an individual any vessel present, whether or not it occurred as a solitary vessel or as one component of a radial multiple (Wheeler 1986). The number of solitary vessels as a percentage of the total was also calculated.

Systematic description

Order **ROSALES**

Family **LEGUMINOSAE**

Organ-genus ***CAESALPINIOXYLON*** Schenk, 1890

?***Caesalpinioxylon moragjonesiae*** sp. nov.
(Figs 1–25)

DIAGNOSIS. [Secondary xylem known only]. Vessels diffuse porous, 5 per mm^2, solitary (54–59%) and in radial multiples of 2–8, tangential diameter means 154–173 μm, element length means 225–328 μm, pits bordered and vestured, 4·5–7 μm diameter. Parenchyma mainly vasicentric with some confluences, also marginal and locally banded, strand parenchyma rare and probably crystalliferous. Rays multiseriate, subhomogeneous to heterogeneous III, with few uniseriates, 1–4 cells wide (range 18–55 μm) but predominantly 2 cells wide (28–45 μm), height means 260–300 μm (11–13 cells). Fibres libriform, thin-walled, rarely locally septate, with very infrequent, indistinctly bordered pits. Traumatic axial canals, in tangential series, usually present.

NAME. In memory of Miss Morag Jones, palaeobotanist, who died during the 1979/80 expedition to Mali.

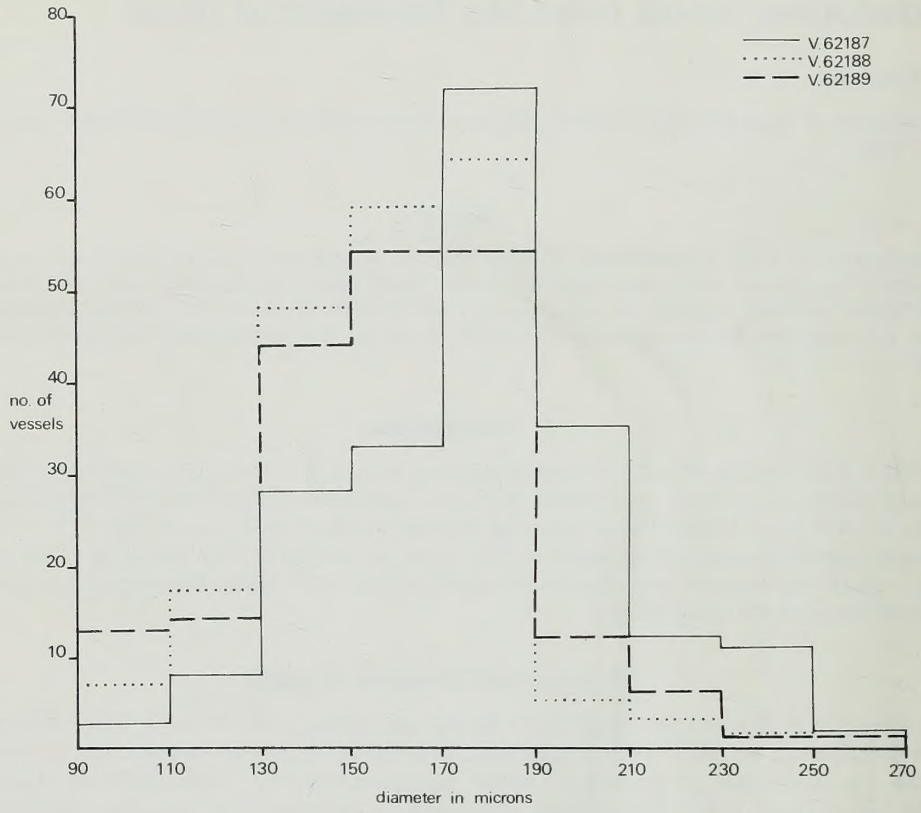


Fig. 1 Vessel tangential diameter in ?*Caesalpinioxylon moragjonesiae* sp. nov. (100 vessels measured per specimen).

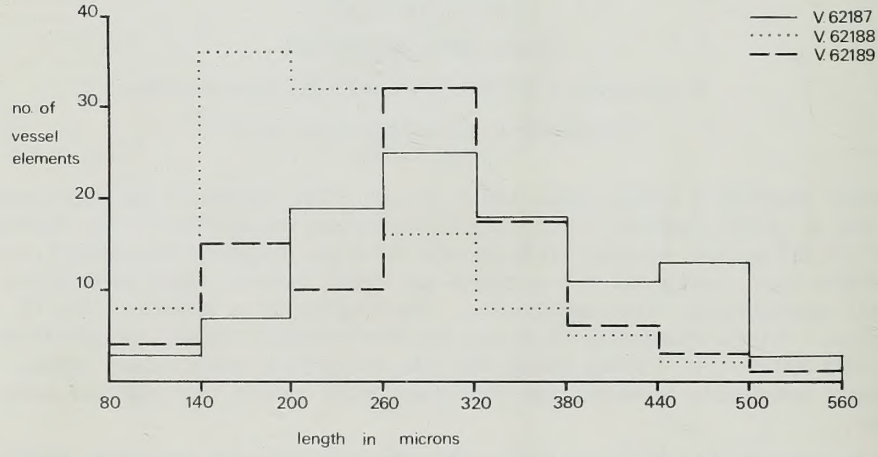


Fig. 2 Vessel element length in ?*Caesalpinioxylon moragjonesiae* sp. nov. (100 vessels measured per specimen).

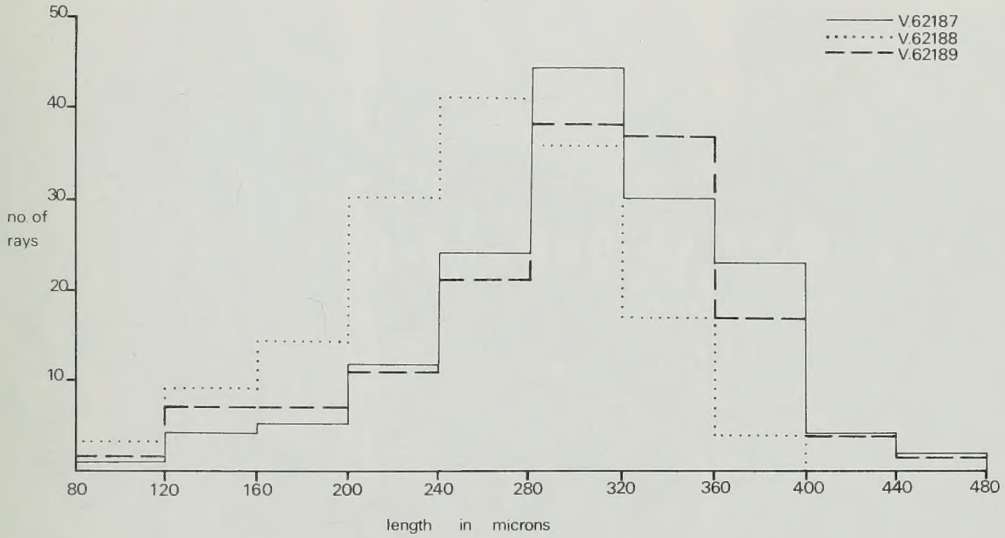


Fig. 3 Ray length in ?*Caesalpinioxylon moragjonesiae* sp. nov. (100 rays measured per specimen).

HOLOTYPE. BM(NH) V.62187 (plus slides a to l and stubs m, n).

OTHER MATERIAL. V.62188 (plus slides a to j and stubs k, l); V.62189 (plus slides a to c).

LOCALITY AND HORIZON. Limestone and calcareous marl deposits. Middle to Upper Palaeocene; Samit, 100 km NE of Gao, Republic of Mali.

DESCRIPTION. *Vessel elements.* Diffuse porous (Fig. 6), solitary 54–59%, remainder in radial

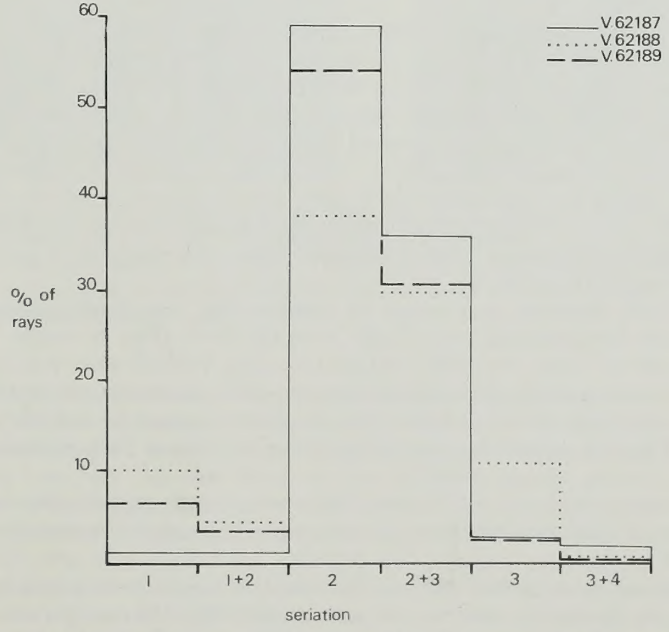


Fig. 4 Ray seriation in ?*Caesalpinioxylon moragjonesiae* sp. nov. (100 rays per specimen).

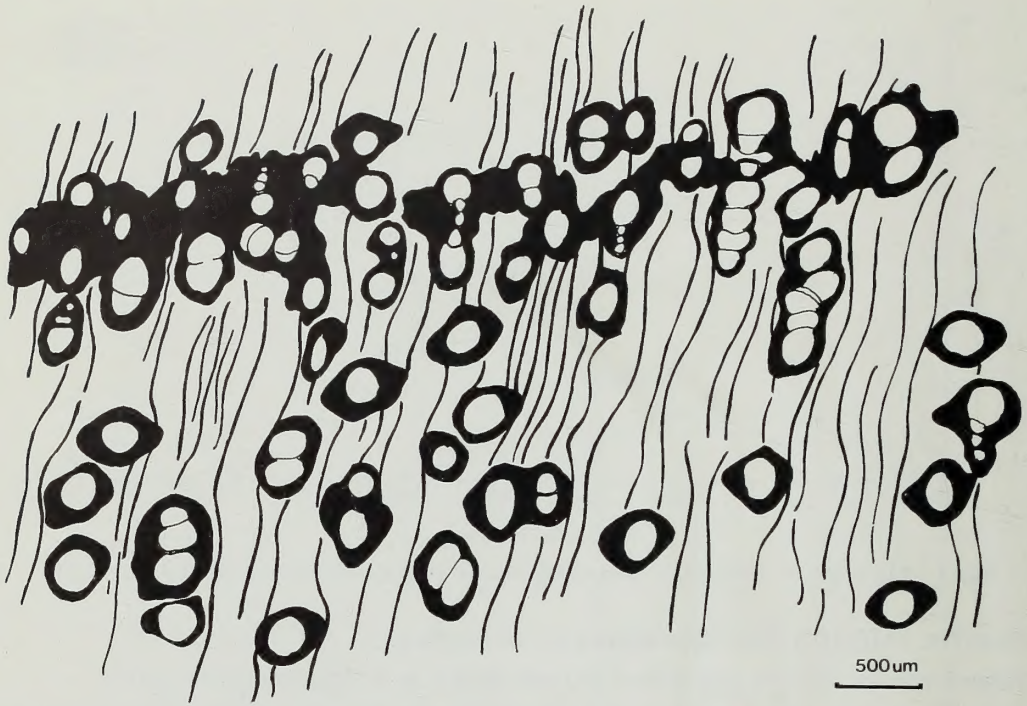


Fig. 5 Transverse section of *?Caesalpinioxylon moragjonesiae* sp. nov., showing terminal parenchyma at top of figure and some paratracheal parenchyma (solid black areas). Sinuous lines show position of rays. Holotype, V.62187.

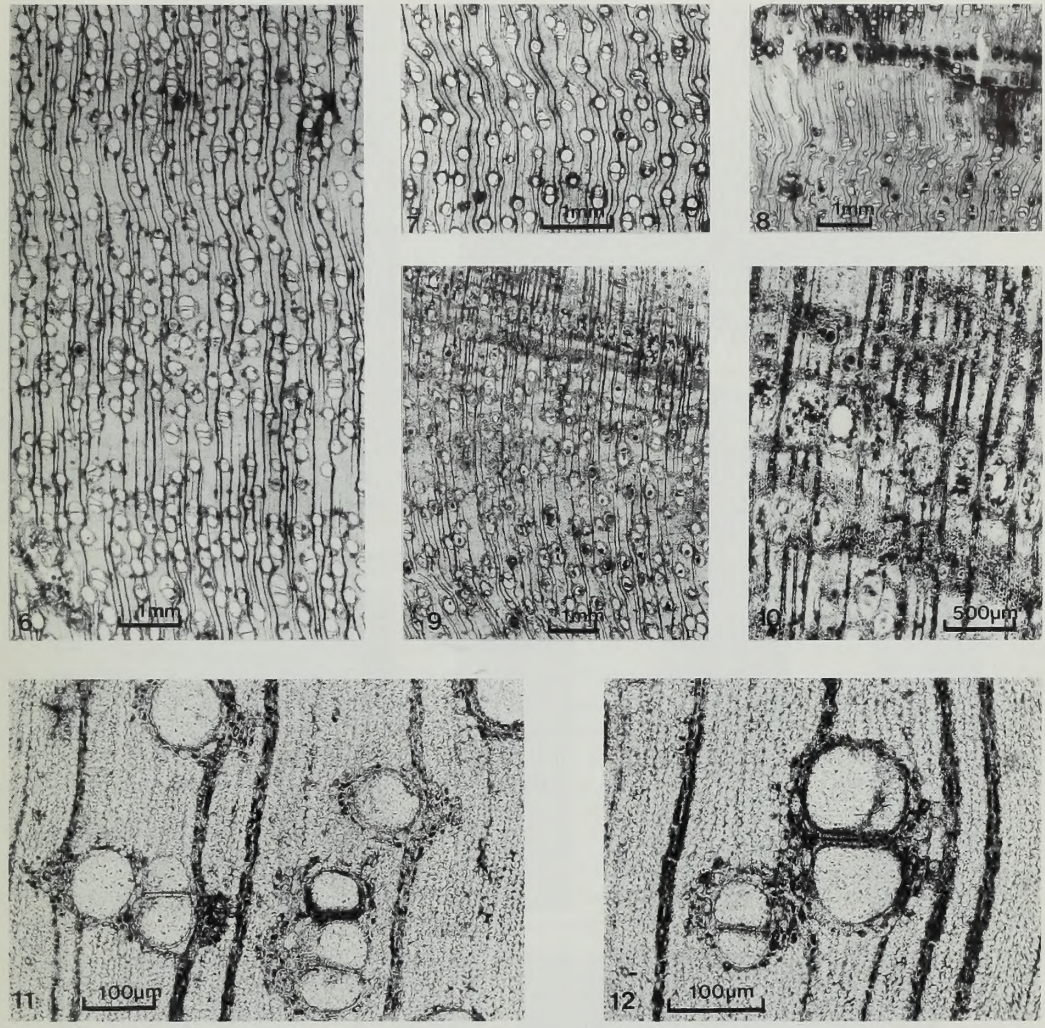
multiples of two to eight; tangential diameter 63–252 μm, mean 154 μm (V.62189), 156 μm (V.62188), 173 μm (V.62187) (Fig. 1); two to ten per mm^2, mean five, length 72–558 μm, mean 225 μm (V.62188), 292 μm (V.62189), 328 μm (V.62187) (Fig. 2); perforation plates simple, horizontal to slightly oblique; intervascular pitting alternate, bordered and vestured, diameter 4·5–7 μm (Figs 18, 23–25); vessel to ray and vessel to parenchyma pitting similar to intervascular.

Parenchyma. Paratracheal: vasicentric to bluntly aliform (sheath up to 6 cells broad), sometimes confluent (Figs 11, 12); apotracheal: infrequent marginal (Fig. 5) and also banded (Figs 9, 10), associated with axial canals; rare chambered cells, composed of at least ten chambers, probably crystalliferous (Figs 15–17).

Rays. Multiseriate, fusiform, commonly *en échelon* (Fig. 14); 8 per tangential mm, range 5–12; 1–4 cells wide but predominantly 2 cells wide (38–54%) (Fig. 4); height 72–504 μm (3–22 cells), mean 260 μm (11 cells, V.62188), 300 μm (13 cells, V.62187 and V.62189) (Fig. 3); subhomogeneous to heterogeneous III; multiseriate rays with uniseriate, marginal rows of radially elongated cells (which are vertically taller than the non-marginal procumbent cells), or square or upright cells (Fig. 13); uniseriate rays infrequent, composed of both procumbent and square cells.

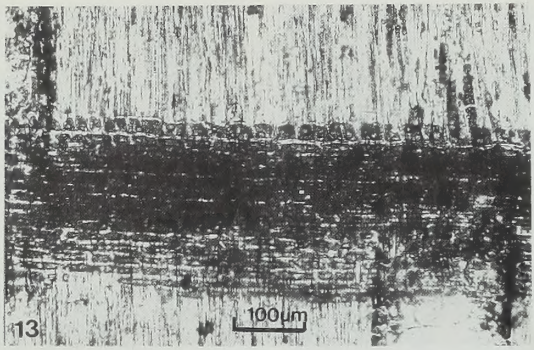
Imperforate tracheary elements. Libriform fibres, rarely locally septate; thin-walled; tangential diameter 6–24 μm; length 500–1035 μm; pits very rare, indistinctly bordered, minute, diameter 2 μm (Figs 19, 20).

Axial canals. Occur in tangential series within bands of apotracheal parenchyma (Figs 8–10); circular to oval in transverse section, tangential diameter 160 μm–300 μm, radial diameter 200 μm to 700 μm; bands of parenchyma 60 μm to 1020 μm (5–37 cells) broad.



Figs 6–12 ?*Caesalpinioxylon moragjonesiae* sp. nov. Fig. 6, TS, diffuse porous vessels with vague zonation; holotype, V.62187b. Fig. 7, TS, diffuse porous arrangement of vessels; V.62188a. Fig. 8, a series of traumatic axial canals, top of figure; V.62188b. Fig. 9, traumatic axial canals with associated banded parenchyma; holotype, V.62187b. Fig. 10, detail of several canals shown in Fig. 9. Figs 11, 12, paratracheal parenchyma; V.62188a.

Discussion. The three specimens are very similar in their qualitative features. Quantitatively V.62188 differs mainly in the lengths of the vessel elements, rays and fibres. Studies by Fegel (1941) have demonstrated a variation in axial element lengths between trunk, branch and root which may be the case here. Another factor in this variation may be growth trauma. The two larger specimens, V.62187–8, show series of axial canals. These were almost certainly traumatic in origin, of the gummosis type formed in response to injury (Record 1925; Barefoot & Hankins 1982). In the canal zone of V.62187 local changes are increased parenchyma, broader rays (up to five cells wide) and medium- to thick-walled fibres. In V.62188 the effect seems more widespread. It has two regions of small vessels, low vessel density and increased paratracheal parenchyma, all similar to that occurring near this specimen's axial canals.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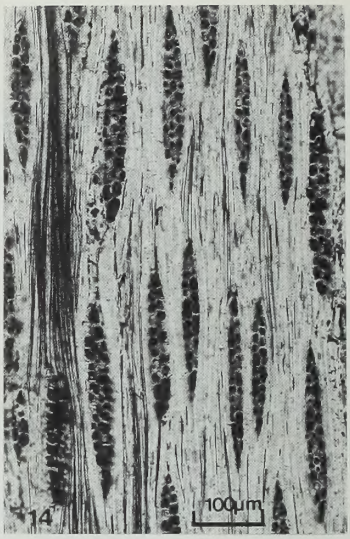
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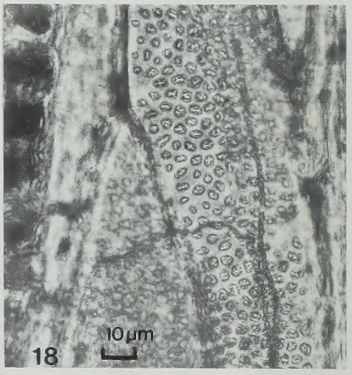
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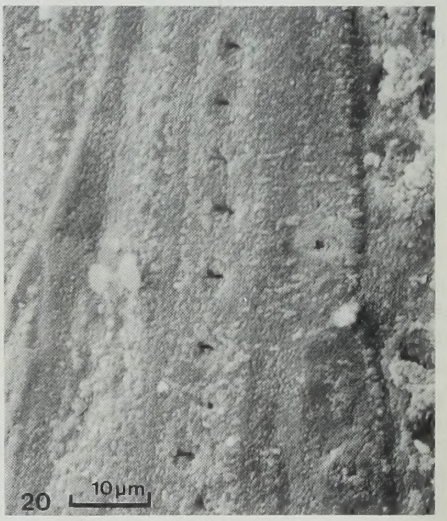
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COMPARISON WITH MODERN GENERA. (All information from Metcalfe & Chalk, 1950, unless otherwise specified). The occurrence of traumatic axial canals and vestured pits is a combination found only in Combretaceae, Euphorbiaceae (Bridelieae only), Leguminosae (except in Dialiinae, Duparquetiinae, Labicheinae and all but one genus in Cercideae), Myrtaceae and Vochysiaceae (Bailey 1933; Record 1936; Quirk & Miller 1983, 1985).

Within Combretaceae the genus *Terminalia* shows many similarities to ?*C. moragjonesiae*, having wood of diffuse porous character, with multiseriate rays and paratracheal parenchyma (van Vliet 1979). Only rarely is there a slight local tendency to irregular stories of rays (Chalk *et al.* 1933). *Terminalia* and other combretaceous woods also differ in their much larger parenchyma cells, greater ratio of uniseriate to multiseriate rays, and larger pitting in the vessels.

In Euphorbiaceae vestured pits occur only in the subfamily Bridelieae. The most similar genus, *Bridelia*, differs in having scanty paratracheal parenchyma, simple vessel to ray pitting and in lacking traumatic canals.

Most genera of Myrtaceae differ from the fossil in possessing vasicentric tracheids and conspicuously bordered fibre-tracheids. The remaining genera have different vessel to ray pitting and no traumatic canals (Ingle & Dadswell 1953).

In Vochysiaceae, *Qualea* is similar to many features but like other genera in the family has simple vessel to ray pitting (Kribs 1959).

Only in Leguminosae do all the features of ?*C. moragjonesiae* occur. Of the subfamilies, the Mimosoideae differ in having entirely homogeneous rays, whilst in 75% of Papilionoideae all the elements are storied (Baretta-Kuipers 1981). The remaining Papilionoideae, which lack or only have some storied structure, and the equivalent in Caesalpinioideae (80%) can be separated by the shape of the terminal cells in the strand parenchyma (Reinders-Gouwentak & Rijsdijk 1955); this is gable-ended in the Papilionoideae but not in the Caesalpinioideae. However, this important feature is not well enough preserved in the fossils to make the distinction. Within the Caesalpinioideae and Papilionoideae traumatic axial canals are recorded in species from the following genera: *Anthonotha* (C.), *Andira* (P.), *Berlinia* (C.), *Brachystegia* (C.), *Cercidiopsis* (C.), *Cryptosepalum* (C.), *Guibourtia* (C.), *Hardwickia* (C.), *Hymenaea* (C.), *Librevillea* (C.), *Macrolobium* (C.), *Michelsonia* (C.), *Microberlinia* (C.), *Monopetalanthus* (C.), *Oddoniodendron* (C.), *Oxystigma* (C.), *Paraberlinia* (C.), *Peltogyne* (C.) and *Tetraberlinia* (C.) (Record 1936; Record & Hess 1943; Brazier & Franklin 1964; Normand & Paquis 1976; E. A. Wheeler and D. Pons, personal communication). They show the following differences when compared with the fossils. *Anthonotha*, *Berlinia*, *Brachystegia*, *Librevillea*, *Macrolobium*, *Michelsonia*, *Microberlinia*, *Monopetalanthus* and *Tetraberlinia* have mainly uniseriate rays. *Guibourtia*, *Hardwickia*, *Hymenaea*, *Peltogyne* and *Oxystigma* have much wider rays. Parenchyma is more abundant and rays are 1–2 seriate in *Oddoniodendron* and *Paraberlinia*. In *Andira* the parenchyma is banded, in *Peltogyne* markedly abaxial and in *Cryptosepalum* markedly more aliform. Material of *Cercidiopsis* was not available for study. Allowing for these differences ?*C. moragjonesiae* is most similar to species of *Tetraberlinia* and *Monopetalanthus*, but not close enough to be considered a fossil representative of either genus. However, its characters show strong affinity with Leguminosae, and most probably Caesalpinioideae.

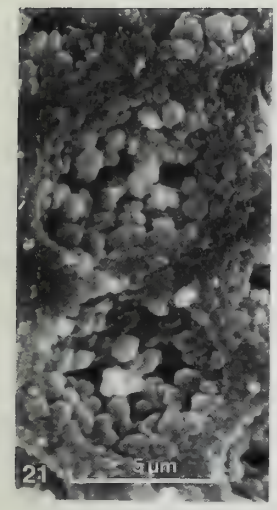
COMPARISON WITH OTHER FOSSIL WOODS. Of the woods assigned to the fossil Leguminosae, only *Erythrophloeoxylon scholleri* (Boureau, 1957) Müller-Stoll & Mädel, 1967 and *Acacia gregorii* Gregory, 1973, exhibit traumatic axial canals. They are compared to ?*C. moragjonesiae* in Table 1, together with *Tetrapleuroxylon ersanense* (Boureau, 1953) Müller-Stoll & Mädel, 1967, the

Figs 13–20 ?*Caesalpinioxylon moragjonesiae* sp. nov. Fig. 13, RLS, wood ray showing a single row of square marginal cells; V.62189a. Fig. 14, TLS of wood rays; holotype, V.62187c. Fig. 15, TLS, chambered parenchyma strands amongst rays and fibres; holotype, V.62187c. Fig. 16, lower parenchyma strand from Fig. 15, showing possible crystal moulds within chambers. Fig. 17, parenchyma strand; holotype, V.62187c. Fig. 18, inter-vessel pitting; holotype, V.62187c. Fig. 19, RLS, fracture plane; some fibres on the right show pitting on the radial surface and those on the bottom left are truncated by a wood ray; holotype, V.62187n. Fig. 20, detail of fibre pitting from Fig. 19; the pits are minute and indistinctly bordered.

Table 1 Comparison of *?Caesalpinioxylon moragjonesiae* sp. nov. with other species of fossil Leguminosae.

Name	*?Caesalpinioxylon moragjonesiae* sp. nov.	*Erythrophloeoxylon scholleri* (Boureau) Müller-Stoll & Mädel	*Tetrapleuroxylon ersanense* (Boureau) Müller-Stoll & Mädel	*Leguminoxylon* (*?Pahudioxylon*) *submenchikoffii* forma *sahariense* Boureau & Koeniguer	*Acacia gregorii* Gregory
Location	Republic of Mali	France	Republic of Mali	Algeria	Oregon, U.S.A.
Age	U. Palaeocene	Oligocene (Stampian)	post-Eocene	Eo-Oligocene	Eocene
Vessels					
distribution	diffuse porous	diffuse porous	semi-ring porous	diffuse porous	diffuse porous
" solitary	54–59	60	60	30–50	mainly solitary
radial multiples	up to 8	up to 4	up to 15	up to 4	up to 3
density	5 per mm^2	2 per mm^2	2–4 per mm^2	3–4 per mm^2	4–11 per mm^2
tangential diameter	63–252 μm	100–200 μm	25–250 μm	210 μm (mean)	100–200 μm
length of vessel elements	72–558 μm	120–250 μm	150–500 μm	190–500 μm	200–400 μm
perforation plate	simple, horizontal –oblique	simple, horizontal	simple, horizontal–oblique	simple, horizontal	simple, oblique
intervessel pitting	alternate, bordered, vestured; 4·5–7 μm diameter	alternate, bordered probably vestured; 4–7 μm diameter	alternate, bordered; 6–7 μm diameter	alternate, bordered, vestured; 5–6 μm diameter	—
vessel-ray pitting	as intervessel	as intervessel	as intervessel	as intervessel	—
Parenchyma					
paratracheal	vasicentric to bluntly aliform, occasionally confluent	mainly confluent, abundant	aliform to confluent, abundant	bluntly aliform	vasicentric to bluntly aliform, occasionally confluent
apotracheal	1) infrequent marginal 2) banded with canals	1) regular marginal 2) ?diffuse	1) marginal 2) diffuse	infrequent marginal	infrequent marginal
Rays					
seriation	(1)-2-(3)-(4)	(1)-2-(3)	(1)-2-(3)	(1)-2-(3)	(1)-(2)-(3)-4-6
tangential density	8 per mm	6–7 per mm	8–9 per mm	7–8 per mm	5 per mm
cellular composition	sub-homogeneous to heterogeneous III	homogeneous to heterogeneous II	heterogeneous II	homogeneous	homogeneous
length	72–504 μm	80–400 μm	up to 540 μm	100–400 μm	30–40 cells high
distribution	commonly *en échelon*	locally storied	locally storied	*en échelon*	diffuse
Fibres					
type	libriform, thin-walled, rarely septate	libriform, thin-walled	libriform, thin-walled	libriform, thin-walled	libriform, thick-walled
pitting	rare, minute bordered	probably simple	probably simple		–
axial canals	large, in apotracheal banded parenchyma	small, in apotracheal banded parenchyma	not present	not present	small, in apotracheal banded parenchyma

Figs 21–25 *?Caesalpinioxylon moragjonesiae* sp. nov.; TLS fracture planes (SEM pictures). Fig. 21, pit detail destroyed by coarse recrystallization; V.62188k. Fig. 22, poorly defined structures in pit chambers; holotype, V.62187m. Fig. 23, vesture-like structures extending into the pit chamber from inside the pit aperture; part of the structure is destroyed by the kind of alteration shown in Fig. 22; V.62188k. Fig. 24, vesture-like structures proliferating within the pit chambers; holotype, V.62187m. Fig. 25, anastomosis of vesture-like structures along the plane of the pit membrane; holotype, V.62187m.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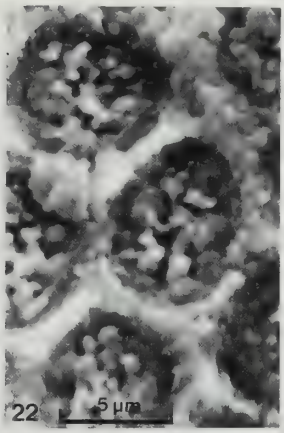
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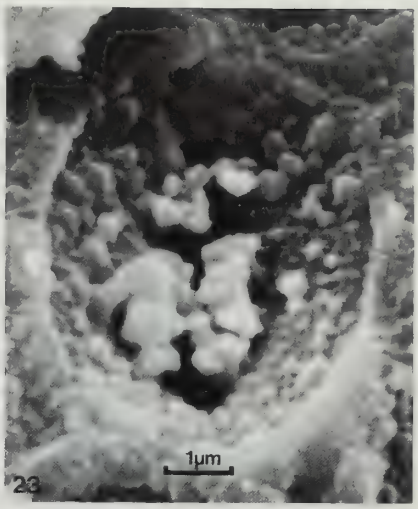
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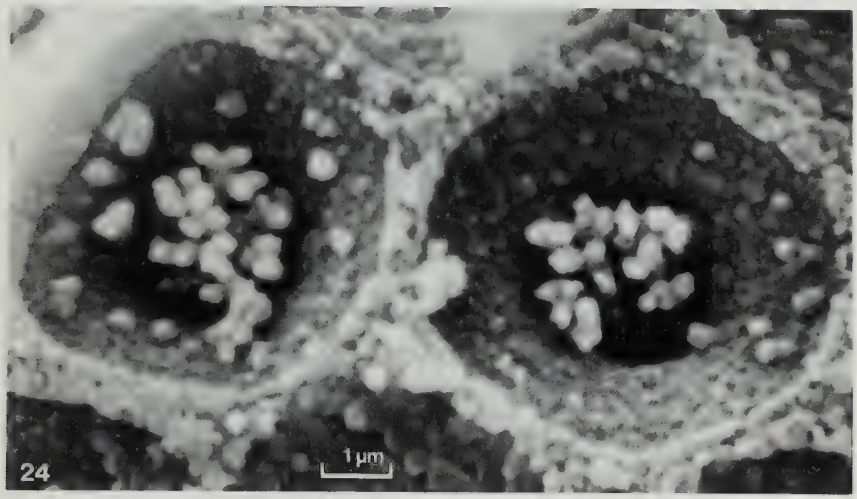
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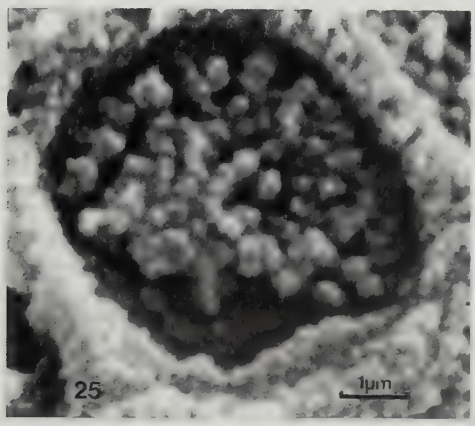
25
1µm

only other Leguminaceous wood from Mali, and *Leguminoxylon* (?*Pahudioxylon*) *submenchikoffii* forma *sahariense* Boureau & Koeniguer, 1970. The latter species is closely comparable with the new Mali wood but lacks traumatic canals. This feature appears sporadically, in keeping with its pathological origins, and may therefore not appear in a fossil species based on one specimen, as with *L. submenchikoffii* forma *sahariense*. In their major revision of fossil leguminaceous wood, Müller-Stoll & Mädel (1967) anticipated the possible appearance of this feature in twelve genera, including *Pahudioxylon menchikoffii* (Boureau, 1951), a species close to *L. submenchikoffii* forma *sahariense*. However, as can be seen from the table, ?*C. moragjonesiae* is distinct from the latter species in having vessels of smaller tangential diameter and a higher proportion of solitary vessels, and in its subhomogeneous to heterogeneous III rays.

Vestured pits in fossil wood. The International Association of Wood Anatomists glossary (1964) defines a vestured pit as 'a bordered pit with the pit cavity wholly or partially lined with projections from the tertiary wall'. Bailey (1933), in an extensive study of pits in Recent woods, showed that vestured pits occur in all or some of the genera within 24 dicotyledonous families. He also described various types of vesture based on light microscopy. Scanning electron microscopy has been used subsequently to confirm and extend Bailey's observations on Recent woods (Meylan & Butterfield 1974; Ohtani & Ishida 1976; van Vliet 1978).

The affinities of some fossil woods have been decided, at least in part, from light microscope investigations of vestured pits (Louvet 1966, 1972; Koeniguer 1966, 1973; Delteil-Desneux 1972). Koeniguer mentions problems in identifying this feature and suggests the possibility of alteration during fossilization.

In studies of Recent wood Bailey (1933), Gale (1982) and Quirk & Miller (1985) described structures simulating vestures ('pseudovestures'). SEM was used to establish whether pitting was vestured or pseudovestured, where this had proved difficult to interpret using light microscopy. Barefoot & Hankins (1982) suggest that vestures should, therefore, be used with care for identification. This problem is compounded when effects of fossilization are taken into account. However, extremely clear illustrations of vestured pits in pyritized fossil wood have been obtained recently by the use of SEM (H. P. Wilkinson, personal communication), and what I believe to be vestured pits in silicified wood are described here for the first time, also on the basis of SEM (Figs 23–25).

Vessels observed on fracture surfaces of ?*C. moragjonesiae* show many areas of pitting. Often these are either coarsely recrystallized (Fig. 21) or show structures too ill-defined to permit critical examination (Fig. 22). In some pits or parts of pits, however, preservation is very much better, showing structures which are closely comparable with the vestures in Recent woods. In Fig. 23 branching structures can be seen emanating from just inside the pit aperture into the pit chamber, towards the site of the pit membrane. These compare closely with the Recent vestures illustrated by Gale (1982: fig. 9) and van Vliet (1978: fig. 22; 1979: pl. 2, fig. 7). In other pits the branching has proliferated within the pit chamber (Fig. 25) in a similar fashion to those illustrated by Ohtani & Ishida (1976: figs 30 & 32). Anastomoses of these structures can be seen in Fig. 24, again comparable to the Recent vestures illustrated by Ohtani & Ishida (1976: figs 29, 38, 45). These authors have shown that several types of vesture are present within the pits of Recent woods, varying from the simplest near the pit border to more massive and complex at or inside the pit aperture. This diversity is also shown by structures seen in Fig. 25. These fossil structures fall well within the size maxima of Ohtani & Ishida for Recent vestures. Some well-preserved pits in the fossil have no vesture-like structures, because, just as in Recent woods, the vestures may be absent from some of the pits in the vessel to ray or vessel to parenchyma pit fields (Ohtani & Ishida 1976). The fact that no similar structures could be found within the inter-pit areas on the outer vessel walls of ?*C. moragjonesiae* again agrees with findings based on Recent woods. Further studies of vestured pits by scanning electron microscopy may assist classification of fossil woods at family and subfamily level.

Acknowledgements

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New palaeontological studies on the Chapelcorner Fish Bed (Upper Eocene, Isle of Wight)

J. Gaudant[1] **and W. J. Quayle**[2]

[1] 17 Rue du Docteur Magnan, 75013 Paris (France)
[2] 51 Whites Road, Bitterne, Southampton SO2 7NR

Summary

Recent excavations in the Chapelcorner Fish Bed (Osborne beds, Upper Eocene) of the Isle of Wight have yielded new specimens of crustaceans and fishes. A more complete description of the prawn *Propalaemon osborniensis* Woodward is given while it is suggested that the specimens previously referred to *P. minor* Woodward are really young of *P. osborniensis* Woodward. Three fish species have also been identified. The most abundant is a clupeid originally described as *Clupea vectensis* Newton; the new genus *Vectichthys* is created for it. The second is a relatively scarce gobiid which resembles *Pomatoschistus* (?) *bleicheri* (Sauvage), from the Lower Oligocene of Alsace. Isolated scales and vertebrae of a species of amiid have also been found.

Prawns and fishes from the Chapelcorner Fish Bed suggest brackish water conditions, and less explicitly that the climate was tropical to subtropical, during the deposition of the fossiliferous clay.

Introduction

The occurrence of fossil fishes and prawns in the Osborne beds of the Isle of Wight was first noted by Colenutt (1888). The fishes were initially studied by Newton (1889), who erected the species *Clupea vectensis*, subsequently transferred to the genus *Diplomystus* Cope by A. S. Woodward (1901). Newton (1899) also distinguished two species among the amiid remains found in the Osborne beds. Moreover, H. Woodward (1903) described two new species of prawns, *Propalaemon osborniensis* and *P. minor*.

All the new material described in this paper comes exclusively from Colenutt's bed 3, better known as the 'Fish Bed', or more precisely as the Chapelcorner Fish Bed (Gamble 1982). Most of it has been found on the shore near Chapelcorner Copse, east of King's Quay Creek, about 3 miles ESE of East Cowes. Some specimens were collected from the shore below Ryde House and Binstead House (west of Ryde) and from Sea View Point (Fig. 1).

The fossils are preserved in a grey-blue shaly clay belonging to the Osborne beds which underlie the Bembridge limestone outcropping in the upper part of the cliff. The stratigraphical position of the Osborne beds has long been controversial, as the Eocene–Oligocene boundary was not clearly defined. Nevertheless, they belong to the Headonian continental stage consid-

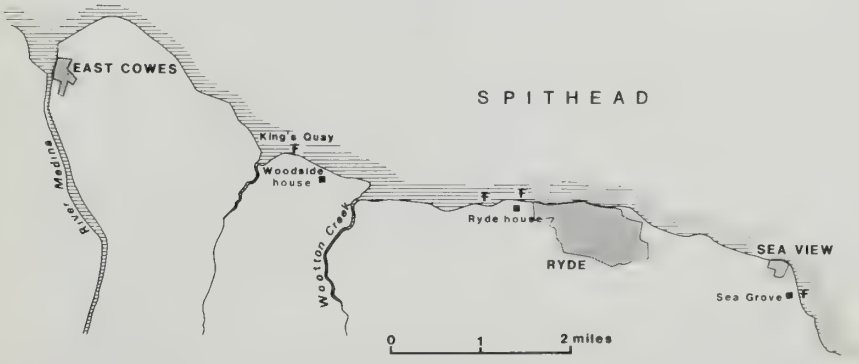


Fig. 1 Map showing the main fossiliferous outcrops of the Chapelcorner Fish Bed.

ered as being the equivalent of Bartonian and Priabonian marine stages. So, their age must be considered as Upper Eocene, the Eocene–Oligocene boundary being placed between the Bembridge marls and the Lower Hamstead beds in the Hampshire basin (Cavelier 1979). Within the lithostratigraphic nomenclature proposed by Insole & Daley (1985) the Chapelcorner Fish Bed is contained within the Fishbourne Member of the Headon Hill Formation, Solent Group. Details of the section may be found in Insole & Daley (1985: 84, fig. 17).

Repositories

Fossils described in this paper are kept in the following museums: British Museum (Natural History), Department of Palaeontology, London (BMNH); British Geological Survey, Keyworth (BGS); Sedgwick Museum, Cambridge (SMC); University of Manchester Museum, Department of Geology (UMMG); and Isle of Wight County Geological Museum, Sandown (IWCGM). All figured specimens are in the BMNH—prefixed by I, In or P—except Fig. 10C.

Explanation of abbreviations used in figures

Ab S	abdominal somite	n.a.PU1 to n.a.PU3	neural apophysis of preural vertebrae
Ang	angular	n.a.U1	neural apophysis of ural centrum
Ant	antennules	Op	operculum
As	antennular scale	PHy	parhypural
Che	chela	Pl	pleopod
Chy 2	posterior ceratohyal	Pmx	premaxilla
Cl	cleithrum	Pop	preoperculum
d.c.s.	dorsal caudal scute	Psph	parasphenoid
Dent	dentary	PT	post-temporal
E	eye	PU_1 to PU_3	preural vertebrae
Ecpt	ectopterygoid	$PU_1 + U_1$	uro-terminal complex
Enpt	entopterygoid	Q	quadrate
Ep, Ep 1–3	epurals	R	rostrum
Fr	frontal	R br.	branchiostegal ray
f.t.	temporal fossa	SCl	supracleithrum
h.a.PU2 to h.a.PU3	haemal apophysis of preural vertebrae	Smx_1, Smx_2	supramaxillary bones
Hmd	hyomandibular	Sop	suboperculum
Hy 1 to Hy 6	hypurals	Sy	symplectic
I	unbranched principal ray of the caudal fin	T	telson
		U1, U2	ural centra
Iop	interoperculum	Un1 to Un3	uroneurals
Iorb.l	lachrymal	Uro	uropod
Mx	maxilla	v.c.s.	ventral caudal scute

Systematic description: Crustaceans

W. J. Quayle

Infraorder **CARIDEA** Dana, 1852

Family **PALAEMONIDAE** Rafinesque, 1815

Genus ***PROPALAEMON*** Woodward, 1903

Propalaemon osborniensis Woodward, 1903
Figs 2–4

1903 *Propalaemon osborniensis* H. Woodward: 98; pl. 5, figs 1–4.
1903 *Propalaemon minor* H. Woodward: 98; pl. 5, figs 5–7.
1925 *Propalaemon osborniensis* Woodward; Woods: 4; pl. 1, fig. 2.
1925 *Propalaemon minor* Woodward; Woods: 5.
1929 *Propalaemon osborniensis* Woodward; Glaessner: 340.
1929 *Propalaemon minor* Woodward; Glaessner: 340.

LECTOTYPE. Of the original material upon which H. Woodward based his description of *P. osborniensis* only one specimen (BMNH In.24494) has been located and is here designated **lectotype**.

MATERIAL. BMNH In.24494 (lectotype), I.4856–7, In.61764–78, In.61687–99; SMC C.23660–1.

H. Woodward based his description of *Propalaemon osborniensis* on 29 specimens collected by Colenutt and Hooley. All the specimens came from the Osborne beds of the Isle of Wight: the majority from Chapelcorner Copse between King's Quay and Wootton Creek. The remainder came from the shore below Ryde House, Binstead House and south-east of Sea View Pier. Unfortunately there is no indication that the specimens in the Sedgwick Museum were included among the original material.

[In a letter to the senior author, Dr G. F. Elliott writes that the late A. G. Davis, who died in 1957, had told him that, when looking for specimens which belonged formerly to Colenutt (who died in 1944), he had succeeded in locating Colenutt's cabinet in Ryde (Isle of Wight). However, the landlord of the house informed Davis that the fossils had been thrown away as they seemed to be devoid of commercial value.]

REMARKS. In his description H. Woodward (1903) divided the prawns into two groups, of large and small individuals respectively. The large specimens (carapace length 20 mm, Fig. 2A) he described as *P. osborniensis*. The smaller ones ('26 mm in length of which the carapace measures 10 mm') he thought could be young forms of *P. osborniensis*, but since there was no positive evidence available, he considered it convenient to treat them as a distinct species, to which he gave the name *P. minor*. Both Woods (1925: 5) and Glaessner (1929: 340) were inclined to agree with this opinion.

Among the recently collected material are specimens equivalent in size to *P. minor* (BMNH In.61692, In.61694, In.61695: Fig. 2C) which however show details of the rostrum, pleopods, abdomen and antennal scale not readily available to H. Woodward and which compare favourably with *P. osborniensis*. *P. minor* Woodward is therefore here considered a junior synonym of *P. osborniensis* Woodward; the latter has been designated by Woods (1925) as the type species of the genus *Propalaemon* Woodward.

Woods (1925) remarked of *P. osborniensis* Woodward that 'the specimens examined by Woodward were very imperfect and owing to subsequent changes in the matrix, have become even more indistinct: at present no other specimens can be obtained and consequently it is not possible to give a diagnosis of the species or to discuss its generic position'. The diagnosis proposed by Glaessner (1969), however, is fundamentally sound. The specimens are preserved in a grey-blue shaly clay and it is evident by comparison with recently-collected material from the type localities that little, if any, change in the matrix of the original material has taken place.

Since the new material shows features not present on the specimens examined by H. Woodward, a revision of the description, incorporating his original observations where appropriate, is given.

DESCRIPTION. The size of the prawns varies from a few millimetres up to 60 mm in overall body length.

The upper margin of the rostrum is lined with six even-sized, sharp, triangular teeth. The first tooth occurs just posterior to the orbit and from there the rostrum (seen to advantage on In.61687 and in In.61766: Fig. 2B) slopes gently upwards as in the Recent forms of *Palaemon*. The underside of the rostrum tapers slightly towards the tip and on In.61766 two teeth can be seen distally. Two specimens (In.61766, In.61770) show that the tip of the rostrum was bifid; the lower member protrudes and is twice the size of the upper.

The antennules are three-flagellate. The outer pair are long, whilst the median one, although shorter, extends beyond the tip of the antennular scale (In.61764). The antennar flagella are long, but their full length cannot be seen on any of the specimens examined. On most specimens an antennal scale is present; the outer margin, straight for most of its length, curves inwards at the tip. The inner margin is straight proximally and tapers gradually until the widest part is reached at one-third the length. At this point it curves inwards and the width decreases

to the tip; the edge is 'feathered' with fine setae. The length of the scale on a specimen with a carapace length of 16 mm is 12·5 mm. On In.61764 and In.61692 can be seen what is possibly an antennal scale.

The posterior margin of the carapace is bordered by a ridge; on the branchial region parallel to this ridge there is a line of small, evenly-spaced pits with some isolated pits parallel to them (In.61689).

The uropods are slightly longer than the telson, with the margin of the telson being simple (In.61690: Fig. 3A). The pereiopods as far as preserved are long and slender, the first and second limbs being chelate (In.61765: Fig. 3B); the chelae of the second pereiopods are three times the length of the chelae of the first pereiopods. The distal joint of the third maxilliped is acuminate and has a line of pores running along the outer margin (In.61691).

According to H. Woodward (1903), the pleopods of one specimen (the lectotype In.24494) were said to be 12 mm in length and the ambulatory legs 25 mm. Two specimens, In.24494 and I.4856, show that the pleuron of the second abdominal somite overlaps that of the first and third pleura. A single spine on the hepatic region could be observed (Woodward 1903: figs 2, 4), and among the recently collected material In.61689 shows the base of what was probably a spine in this area. Owing to the way the material is preserved, no further details of the abdomen could be observed.

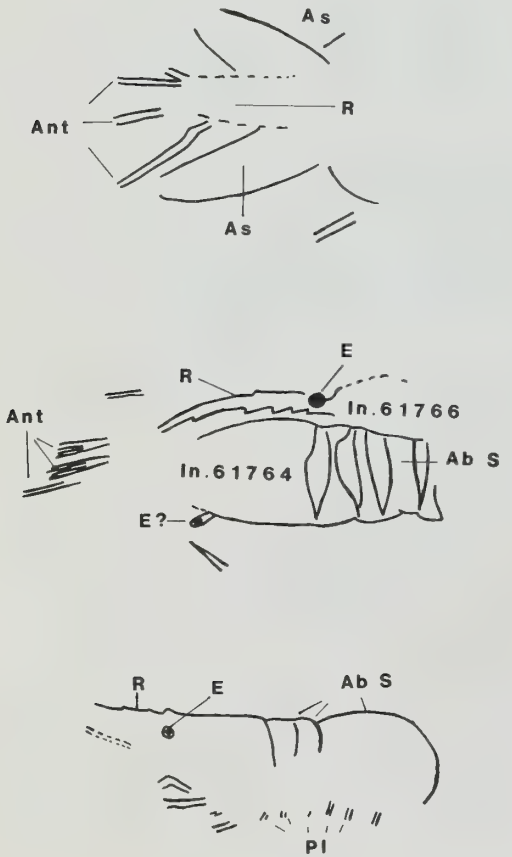
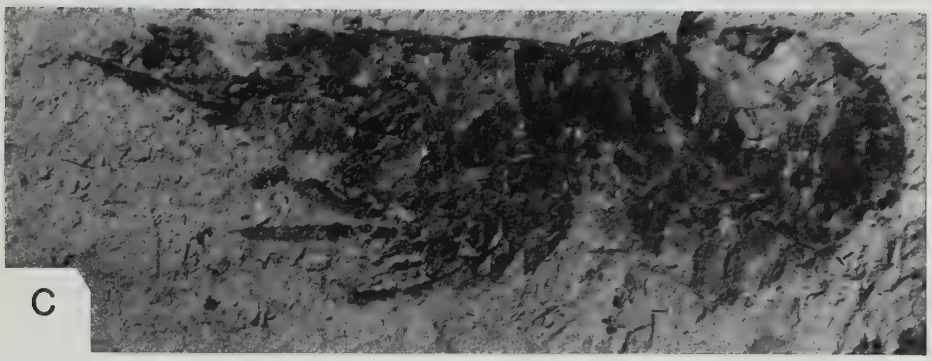


Fig. 2 *Propalaemon osborniensis* Woodward. A, anterior portion showing antennules and antennular scale. In.61688 preserved in a dorsoventral position (×5·5). B, In.61764 preserved in a dorsoventral position showing antennules, eye, and somites. In.61766 lying alongside preserved in a lateral position, showing upper margin of rostrum (both ×2·4). C, In.61695 (×5·5) preserved in left lateral view.

A

B


C

Discussion. H. Woodward (1903) stated 'the bifid flagella of the inner antennae are preserved in fig. 1 and fig. 2'. These are possibly the inner and outer flagella while the shorter median one is hidden between them. In the new material this smaller flagellum is present on two specimens (In.61688, In.61764: Fig. 2A, B) which are preserved crushed in a dorsoventral position rather than in the more customary lateral attitude. It is possible that only specimens in the latter position were available to H. Woodward.

It appears that the carapace size quoted by H. Woodward included the rostrum (1903: fig. 1, carapace 20 mm). In the above description the carapace length was measured from the hinder margin of the orbit to the posterior margin.

Relationships. Houša (1956) described a new genus, *Bechleja*, but no doubt owing to the state of preservation of available material much information appears to be lacking from the comparisons he made with other known fossil palaemonid prawns. Feldmann *et al.* (1981) described *Bechleja rostrata* from the Green River Formation, U.S.A.; this and the present redescription of *Propalaemon* should help to fill in some of the missing information. The following are the main differences between these two genera. *Bechleja*, according to Houša (1956), has a single filament antennule; Feldmann *et al.*, however, suggest there are two, whereas *Propalaemon* has three filaments. The main differences according to Houša (1956) are that the telson and uropods of *Propalaemon* are proportionately larger.

Houša (1956) also states that *Palaemon exul* Frič should not be included in the genus *Palaemon*, 'because it differs from it by several important characters' which he did not clarify. According to Glaessner (1969) the generic diagnosis for *Palaemon* is: 'carapace with antennal and branchiostegal spines; no hepatic spines; antennules three flagellate; telson with four apical spines'. Comparing this with the description by Frič (1872), wherein no mention is made of either antennal or branchiostegal spines, the antennules have two flagellae and the telson lacks apical spines. In addition the fifth pair of pereiopods are stronger and twice the length of the previous pair. Additional well preserved material will undoubtedly support the opinion of Houša (1956) that a new genus is required for *Palaemon exul* Frič.

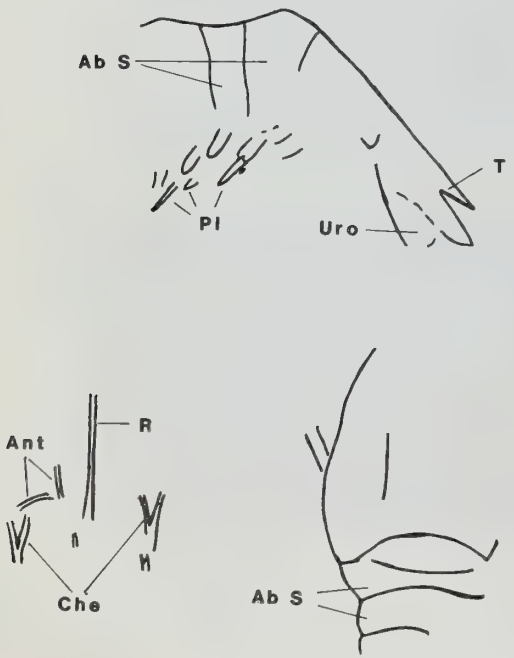
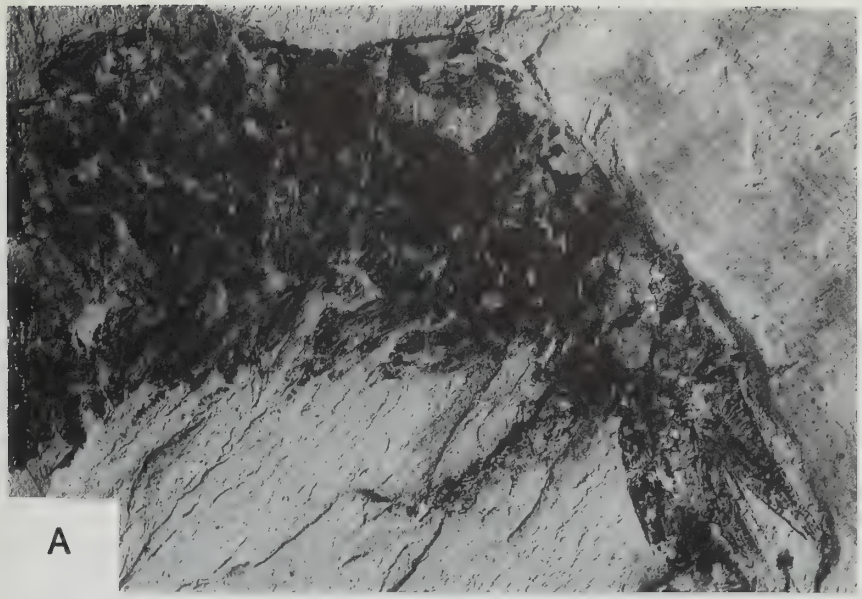


Fig. 3 *Propalaemon osborniensis* Woodward. A, telson, uropods, somites with incomplete pleonites, In.61690 (× 2·3). B, chelae of the second pereiopods, In.61765 (× 2). C, incomplete carapace and parts of first two somites, preserved in a dorsoventral view, In.61689 (× 2·5).


A

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C

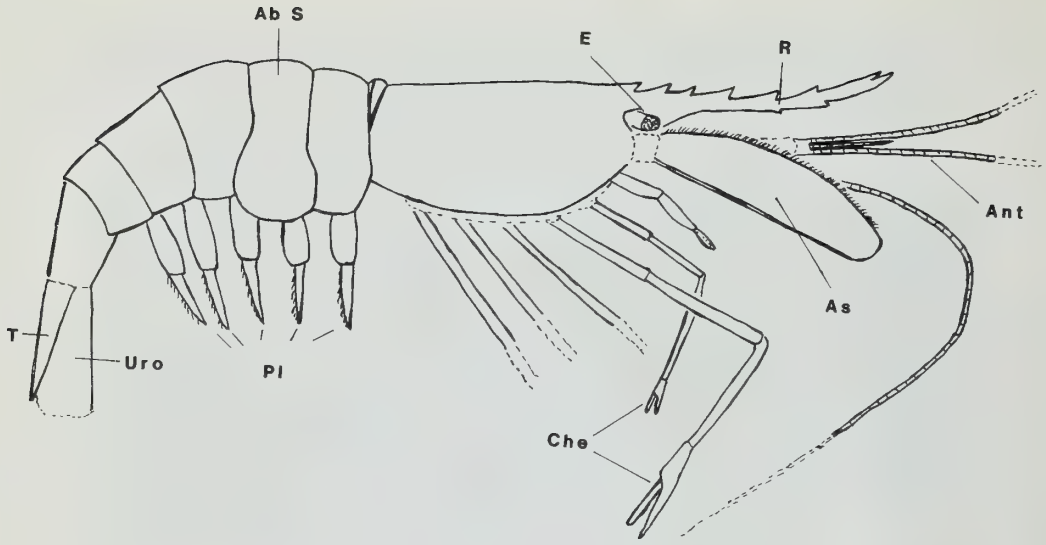


Fig. 4 *Propalaemon osborniensis* Woodward. Restoration in right lateral view.

Systematic description: Fishes

J. Gaudant

Order **AMIIFORMES** Huxley, 1861

Family **AMIIDAE** Bonaparte, 1832

Genus ***AMIA*** Linné, 1766

Amia (?) sp.

Newton (1899) distinguished two species, *A. anglica* Newton and *A. colenutti* Newton, among the isolated amiid remains found in the Chapelcorner Fish Bed. To the first species are referred isolated vertebrae and scales, one premaxillary and several dermal head bones, while a maxillary found in Colenutt's bed 5 is *A. colenutti*. However, it is to be noted here that only three scales figured by Newton (1899: pl. 1, figs 19–21) come from Colenutt's bed 3. From the same bed an isolated amiid scale (BMNH P.59773) and an amiid vertebra (found by Mr Kemp of Gosport) have been found recently.

It is not our purpose to give here a taxonomic reassessment of the amiid remains found in the Palaeogene of the Isle of Wight, as it is clear that the scales and the unique vertebra found in Colenutt's bed 3 to date do not allow specific determination. The isolated abdominal vertebra found by Mr Kemp has a typically ovoid sectional outline, but as it probably comes from the middle part of the abdominal region, it is not particularly significant taxonomically.

Order **CLUPEIFORMES** Bleeker, 1859

Suborder **CLUPEOIDEI** Bleeker, 1859

Family **CLUPEIDAE** Cuvier, 1817

Genus ***VECTICHTHYS*** nov.

Diagnosis. Differs from other clupeoid genera by the following combination of characters: double-armoured herrings with a complete series of ovoid dorsal scutes, each provided with a median longitudinal crest. Two supramaxillaries. Dentary edentulous. Vertebral column relatively short (about 40 vertebrae). Caudal axial skeleton with first preural (PU1) and anterior ural (U1) centra separate.

TYPE SPECIES. *Vectichthys vectensis* (Newton).

NAME. From Vectis, the Latin name of the Isle of Wight.

Vectichthys vectensis (Newton 1889)
Figs 5–12

1889 *Clupea vectensis* Newton: 112; pl. 4.
1901 *Diplomystus vectensis* (Newton) A. S. Woodward: 146.
1982*b* '*Clupea*' *vectensis* Newton; Grande: 14.

NEOTYPE. All the material figured by Newton (1889) must be considered lost (see note, p. 17). So, the specimen BMNH P.62097 is here designated as **neotype** of *V. vectensis* (Newton).

MATERIAL. BMNH P.5930, P.6853, P.6853a–h, j–n, P.6854, P.39302, P.59770–2, P.59777–83, P.59789–96 and P.59798–800; BGS GSM 3131 and GSM 97123–30; SMC C.23604–21, C.23624–31, C.23634–47; UMMG 5562a–e; IWCGM 3242.

DIAGNOSIS (emended). Small species, the total length of which does not generally exceed 60 mm. Body slender: maximum height included 4 or $4\frac{1}{2}$ times in standard length. Head large, its length being about a quarter of standard length or slightly more. Upper jaw toothed, maxillary broad, mandible edentulous, dentary projected upwards. Vertebrae 40–41: abdominal 24–25, postabdominal 15–16. Ribs about 20 pairs. Dorsal fin inserted in middle of body, ii – iii + I + 12 rays. Anal fin low, ii – I + 14 – 17 rays. Pectorals moderate in size, with about 10 rays. Pelvic fins relatively small, inserted opposite the origin of dorsal fin and containing seven rays. Eight or nine ovoid dorsal scutes, each with a short median crest. Abdominal scutes not serrated, decreasing in size backwards.

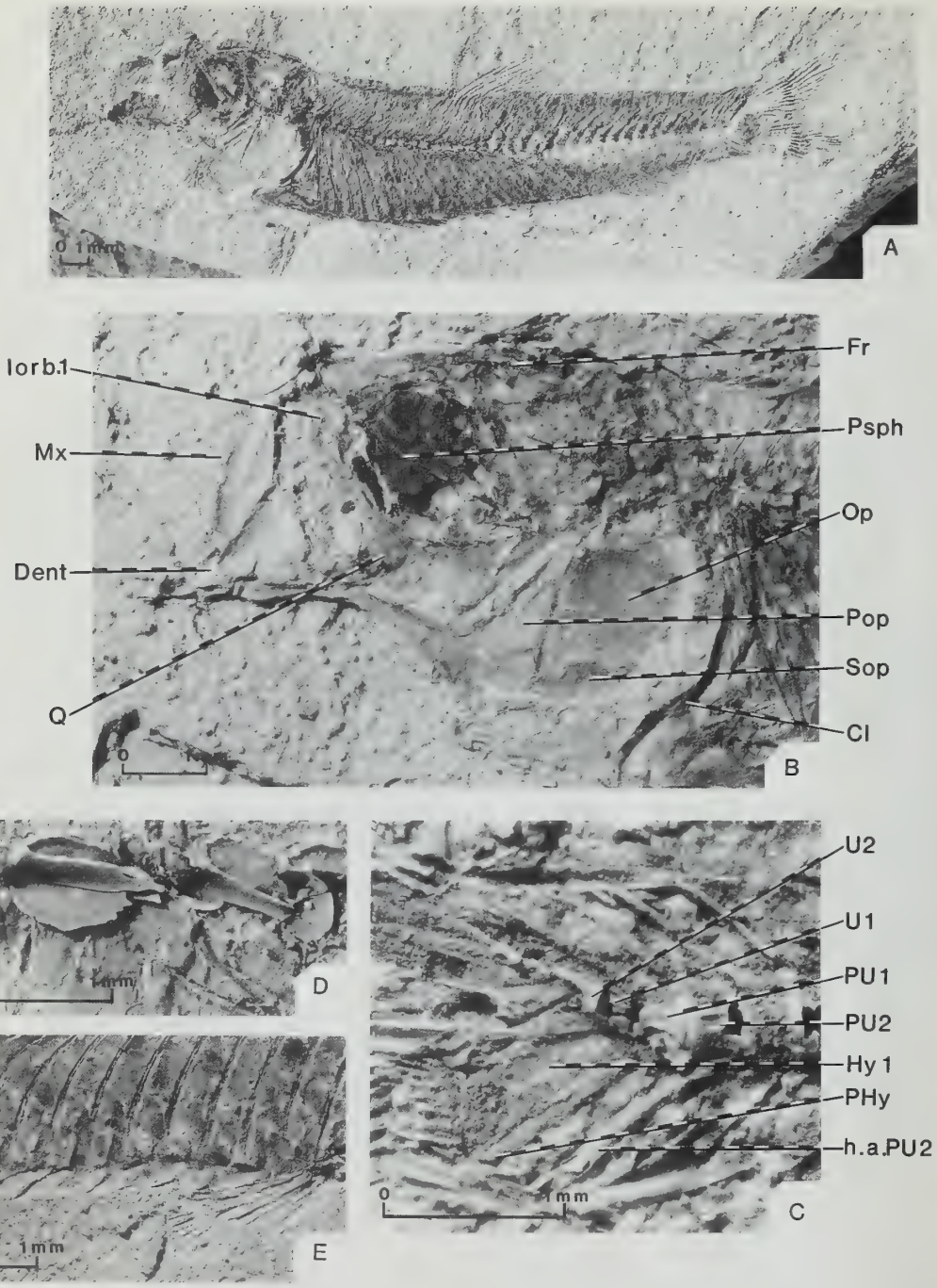
DESCRIPTION. *Vectichthys vectensis* (Newton) is a small species, the total length generally less than 60 mm. (Newton, 1889, described four large specimens between 43 and 58 mm long, while an incomplete specimen collected by one of us [W.J.Q.] is calculated to have had a standard length of 62 mm.) Moreover, two large, poorly preserved fragmentary fishes (one of them with counterpart), the standard length of which must have been about 220 mm, have also been found recently (P.59798–800): identification of these specimens as this species is not however completely certain.

The head is large, being equal to 25–30% of the standard length. The caudal fin is deeply forked and is always shorter than the head; its length is about equal to the maximum depth of body. The dorsal fin is inserted midway along the body or just in front of this level. It lies opposite the pelvic fins which are inserted midway between the pectoral fins and the origin of the anal fin.

Measurements of several well-preserved specimens are on file in the Department of Palaeontology of the British Museum (Natural History).

The head (Figs 5B, 6) is fairly well preserved in P.6853. It is deep, its height being about three-quarters of its length. Little is known of the anatomy of the cranial roof but the well developed frontals are well exposed, extending beyond the posterior edge of the orbit. A temporal fossa is present (P.59793). The orbit is large, the diameter being almost a third of head length. It is surrounded posteriorly and ventrally by the infraorbital series in which only the large lachrymal carrying the infraorbital canal is clearly seen. However, the position of the posterior components of the infraorbital series seems to indicate a *recessus lateralis* into which converge the preopercular, the supraorbital and the infraorbital canals.

The mouth is moderately large, the articulation of the lower jaw occurring beneath the middle part of orbit. The mandible (Figs 6, 7) is well developed and massive: its length is included slightly more than twice in the head length while its maximum height reaches almost half of its length. From the symphysis, the relatively low, toothless, oral edge of the dentary rises rapidly towards the coronoid process, which points sharply upwards (P.6853e, P.62097). The upper jaw (Fig. 8) is composed of a relatively small, elongate, toothed premaxilla, the oral edge of which constitutes less than half the jaw (P.59780). The maxilla is robust and has a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convex oral edge on which small denticulations are present (P.59778). Two supramaxillae are present. The first one, which is rod-like (P.59792), is bordered dorsally by the anterior process of the second one, the hind part of which is expanded (P.6853c).

In the palatoquadrate, the quadrate (Fig. 6, Q) is generally well preserved. As usual, it is triangular in shape and its dorsal side is depressed posteriorly to receive the symplectic. The ectopterygoid displays a typical boomerang shape with two arms, the anterior one being prolonged forwards by the dermopalatine (P.59782). The entopterygoid (Enpt) can also be recognized on P.6853c.

The opercular apparatus is characterized by the large size of the operculum. This bone (Fig. 9A) has a typical posterior outline which is concave between its upper part and its posterior angle. A more or less similar concavity of the posterodorsal edge of the operculum is also present in *Knightia* and *Gosiutichthys* described by Grande (1982*b*).

The rectangular-shaped subopercular is comparatively small. Its size roughly equals that of the interoperculum. The preoperculum (Fig. 9B) is well developed: its lower arm is almost as long as the vertical one, with which it makes an angle of 110° measured along the two parts of the preopercular canal.

The vertebral column is composed of 40–41 vertebrae, 15–16 of which are postabdominal. This number is slightly more than that of *K. eocaena* Jordan (13–15: Grande 1980) while the number of abdominal vertebrae (23–25) may be compared to that known in *K. alta* (Leidy).

All vertebral centra are elongated. They bear long, slender neural and haemal spines, the distal ends of which reach about two-thirds of the distance from the dorsal (or ventral) part of each centrum to the dorsal (or ventral) margin of the body. In front of the dorsal fin, nine slender predorsal bones are present (P.59793).

Epineurals can be seen along the vertebral column while ventral intermusculars are restricted to the postabdominal region. There are about 20 pairs of long, robust ribs. Excepting the last pair all reach the ventral mid-line. In front of the pelvic fins, the abdomen is provided with a series of about 15–16 abdominal scutes of clupeid type, five or six occurring in front of the origin of the pectoral fins. About nine scutes are present between pelvic and anal fins.

In front of the dorsal fin, another series of eight or nine scutes can be observed (following Grande, 1982*b*, about 13 scutes would be present). These dorsal scutes (Fig. 10B) are similar to those of the North American species of *Knightia*. They are ovoid with the anterior part slightly drawn out, while their posterior edge is regularly rounded. They are provided with a longitudinal keel, the anterior end of which projects forwards. The shape of these dorsal scutes does not differ significantly from that of similar elements in *K. eocaena* Jordan (as demonstrated by specimen P.4929, Fig. 10A). The same is true for the dorsal scutes of the Recent Australian pellonuline species *Hyperlophus vittatus* (Castelnau) (Fig. 10C; see also Grande, 1982*a*, figs 25–28), and the clupeines *Gosiutichthys* Grande (1982*b*: fig. 18), *Herklotsichthys*, *Opisthonema* and *Harengula*.

The caudal fin is deeply forked, the length of the innermost principal rays being no more than half the length of the longest ray of each lobe. Ten principal rays (nine of which are both articulated and branched) are present in the dorsal lobe, while nine principal rays (eight of which are both articulated and branched) make up the ventral lobe. In large specimens (P.59798), the segments of the unbranched principal ray of the dorsal lobe of the caudal fin exhibits a typical zigzag shape. It is to be noted that the inner ray of each lobe is inserted more anteriorly than the principal caudal ray, as in most clupeoids. Dorsally and ventrally, six or seven short marginal (procurrent) rays are present. Each series is preceded by a long rod-like scute.

Specimen P.6853 (Fig. 11A) exhibits five preural vertebrae involved in support of the caudal fin rays. Except for the posterior preural centrum (PU1) which bears a short flat neural arch

Fig. 5 *Vectichthys vectensis* (Newton). A, general view of the **neotype**, here designated, P.62097 (× 4). B, head of specimen P.6853 (× 12), see also Fig. 11A. C, axial caudal skeleton of one of the specimens preserved on the slab P.6854 (× 27), see also Fig. 11B. D, dorsal scutes of P.59772 (× 20). E, pelvic fin and ventral scutes of P.6853b (× 8).

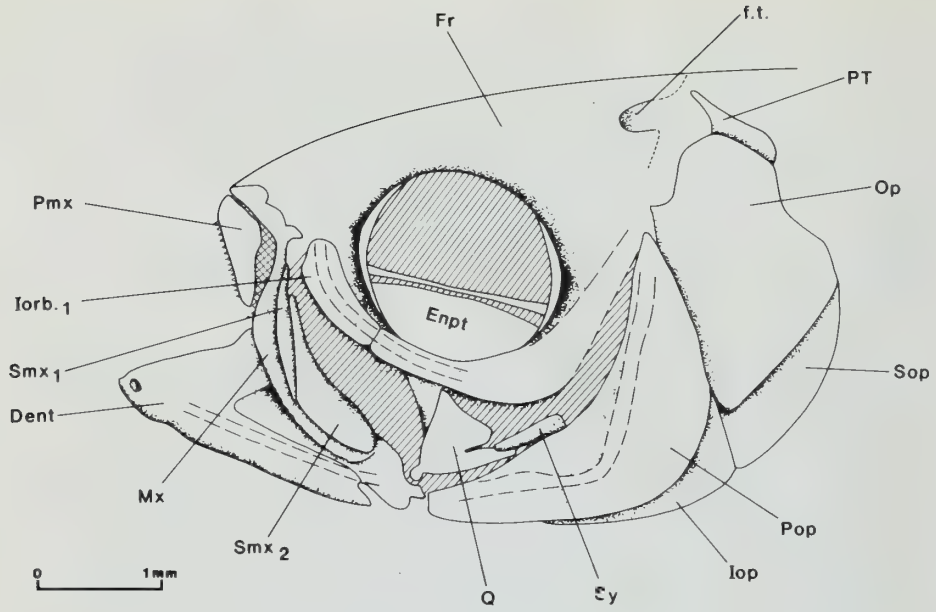

Fig. 6 *Vectichthys vectensis* (Newton). Reconstruction of the head.

(n.a.PU1), they have elongate neural and haemal spines. The neural and haemal spines of PU4 and PU5 bear the dorsal and ventral rod-like caudal scutes.

One of the fishes preserved on the slab registered P.6854 (Figs 5C, 11B) clearly demonstrates that the end of the vertebral column is composed of three modified vertebrae. The least modified is PU1, with which articulates ventrally a narrow parhypural (PHy). The well-developed U1 is followed by a small triangular element which can be interpreted as a second centrum, U2.

As previously noted by Greenwood (1968) in the fossil genera *Knightia* Jordan and *Diplomystus* Cope, the structure of the caudal skeleton described above, in which PU1 and U1 remain separate, is like that known in Recent double-armoured herrings.

Posteriorly, three elongate, rod-like uroneurals (Un1, Un2, Un3) can be distinguished on specimen P.59792 (Fig. 11C). The first one seems to originate on the posterior preural centrum (PU1), as shown by P.6853 (Fig. 11A). The second originates beneath the preceding one, and a third uroneural is also present posteriorly, just above the upper hypural (Fig. 11C).

The two ural centra support six hypurals. The lower one (Hy 1) is by far the broadest. Its proximal end is somewhat pointed and articulates with the ventral part of U1. The second

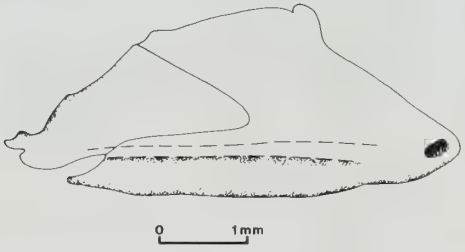

Fig. 7 *Vectichthys vectensis* (Newton). Right lower jaw of P.59779 in lateral view.

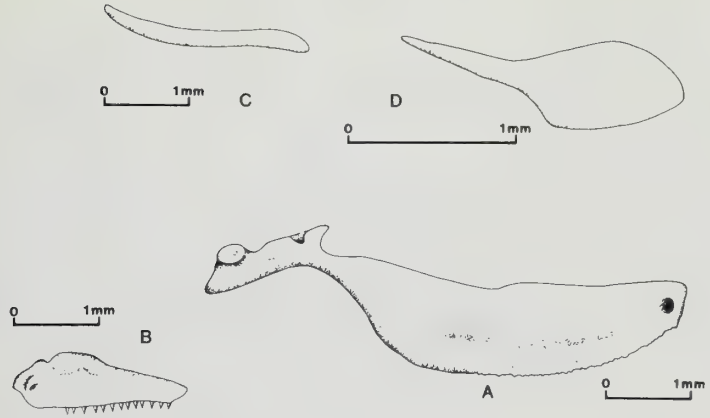

Fig. 8 *Vectichthys vectensis* (Newton). Components of the upper jaw. A, right maxilla (P.59778) in medial view; B, right premaxilla (P.59780) in medial view; C, anterior supramaxilla (P.59792), see also Fig. 11C; D, posterior supramaxilla (P.6853c).

hypural (Hy 2), long and narrow, is fused with the anterior ural centrum (U1). Hypurals 3 to 6 support the upper lobe of the caudal fin. The lowermost (Hy 3) is the widest. Dorsally, PU1 bears a short neural arch (n.a.PU1). Three epurals (Ep 1–3) occur behind the neural arch of PU1 (Fig. 11A, C).

The dorsal fin includes 15 or 16 rays (Newton, 1889, estimated 14 or 15). The first two (rarely three) are short and they are followed by a long articulated ray which is the longest of the fin; its length is about two-thirds of maximum body height. Posteriorly, 12 articulated and branched rays are present. The dorsal fin rays are generally supported by 13 or 14 rod-like pterygiophores which are relatively short, as only the proximal end of the first reaches the distal part of corresponding neural spines.

The anal fin is of moderate size, comprising 16 to 20 fin rays. The first two are short while the third one, which is articulated but not branched, is the longest of the fin. Its length is slightly less than half the maximum height of the body. Posteriorly, there are 14–17 articulated and branched rays. The endoskeleton of the anal fin has 15–18 (occasionally 19) short, rod-like

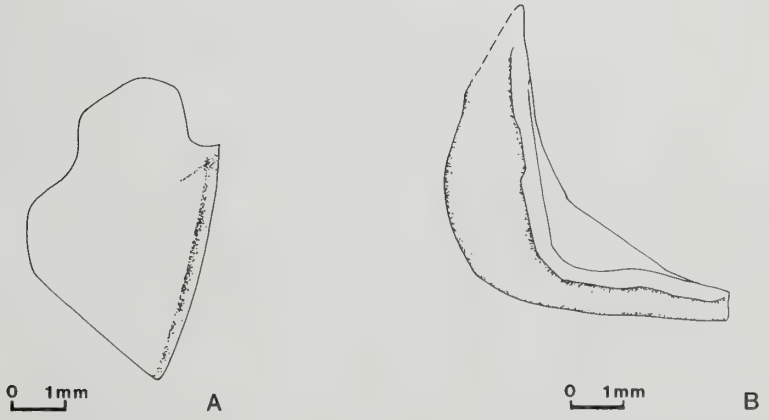

Fig. 9 *Vectichthys vectensis* (Newton). A, right operculum (P.59771); B, preoperculum (P.59790).

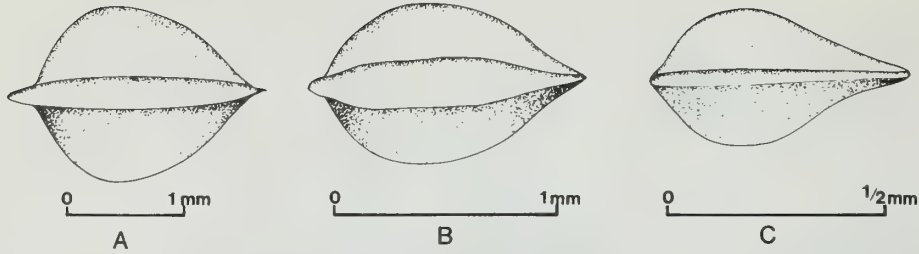

Fig. 10 Dorsal scutes of double armoured herrings. A, *Knightia eocaena* Jordan (P.4929). B, *Vectichthys vectensis* (Newton) (P.59772). C, *Hyperlophus vittatus* (Castelnau). Recent, Australia.

pterygiophores, the proximal ends of which do not reach the distal part of the vertebral haemal spines.

Both the pectoral fins and girdle are imperfectly known. The pectoral fins are of moderate size and contain about ten rays. The cleithrum is generally well preserved. It is characterized by its large vertical arm and its relatively shorter lower arm. The supracleithrum is somewhat slender and articulates dorsally with the bifid post-temporal, the dorsal arm of which is longer than the ventral one.

The pelvic fins are relatively small. Each contains seven rays (Newton, 1889, counted eight or nine rays but this number is clearly inaccurate). They originate midway between the pectorals and the origin of the anal. Their length is equal to about half the distance between their base and the origin of the anal. The pelvic bones are rather slender. Their length is about half that of the fin-rays.

The body is covered with large cycloid scales marked with many circuli which show a largely vertical orientation, characteristic of clupeiform scales. There appear to be about 60–80 circuli per mm (P.59779). As noted by Newton, the lateral line is absent as in all clupeoids. There are about 40 vertical scale rows between the pectoral girdle and the base of the caudal fin. Between the dorsal and pelvic fins about eight longitudinal scale rows may be counted.

Relationships. After its description by Newton (1889), *Clupea vectensis* was transferred by A. S. Woodward (1901) to the genus *Diplomystus* Cope. However, Jordan (1907) noted that Cope (1884) had earlier distinguished two sections within his genus *Diplomystus*. Jordan therefore proposed these sections of *Diplomystus* should each be considered a distinct genus, and that the generic name *Knightia* should be used for species having dorsal scutes 'not wider than long' and bearing 'a single median posterior tooth at the end of a median longitudinal carina'. The name *Diplomystus* Cope (s. str.) was restricted to fishes with 'dorsal scutes . . . transverse with pectinate borders, a median tooth being especially prominent'. So it appears that the clupeid fishes from the Isle of Wight described in this paper are more closely related to *Knightia* than to *Diplomystus*, as these fishes have a complete series of more or less ovoid dorsal scutes.

Recently, Grande (1982*b*) has revised the North American species of *Knightia* Jordan and erected a new allied genus, *Gosiutichthys*. It is thus now possible to use precise data in comparing '*Clupea*' *vectensis* with these fishes. Grande defines the genus *Knightia* as a double-armoured herring with only one supramaxillary bone, 36–40 vertebrae, 20–22 pairs of pleural ribs and 12–14 ovate to circular dorsal scutes. *Gosiutichthys* Grande differs from *Knightia* Jordan in that it has two supramaxillaries and fewer vertebrae (34–36).

Like the North American fossil double-armoured herrings, '*Clupea*' *vectensis* Newton exhibits clupeoid characters in the fusion of the first uroneural with the first preural centrum and the lack of a lateral line. However, as exhibited by the specimen P.6854, the first ural centrum seems to have been larger than in the three North American species of *Knightia*. Moreover, '*Clupea*' *vectensis* Newton differs from them as it has two supramaxillaries, an edentulous dentary and fewer dorsal scutes (8–9 against 10–14). The English fossil herring differs also from *Gosiutichthys* Grande in its meristic characters: it has more vertebrae (40–41 against 34–36),

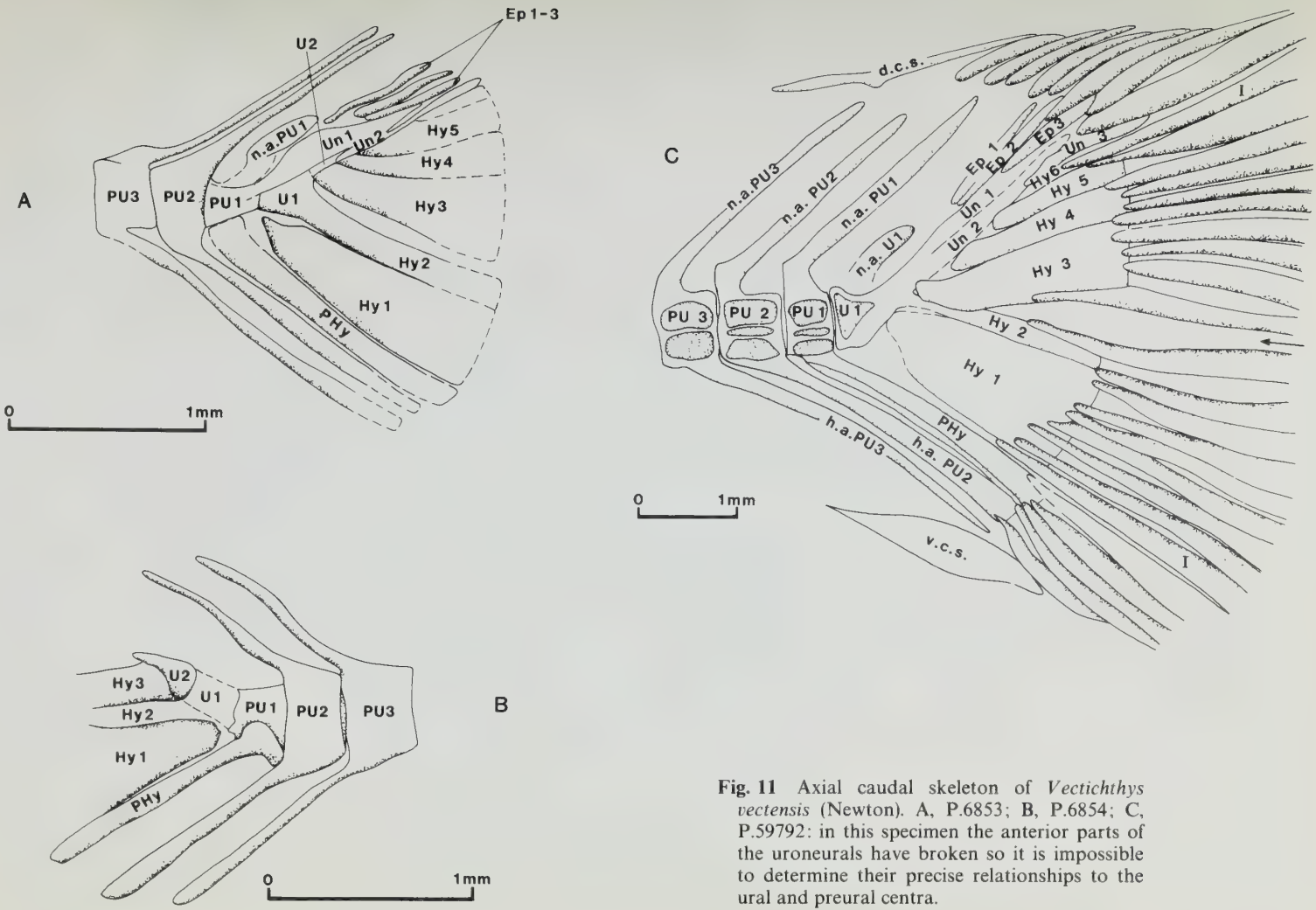

Fig. 11 Axial caudal skeleton of *Vectichthys vectensis* (Newton). A, P.6853; B, P.6854; C, P.59792: in this specimen the anterior parts of the uroneurals have broken so it is impossible to determine their precise relationships to the ural and preural centra.

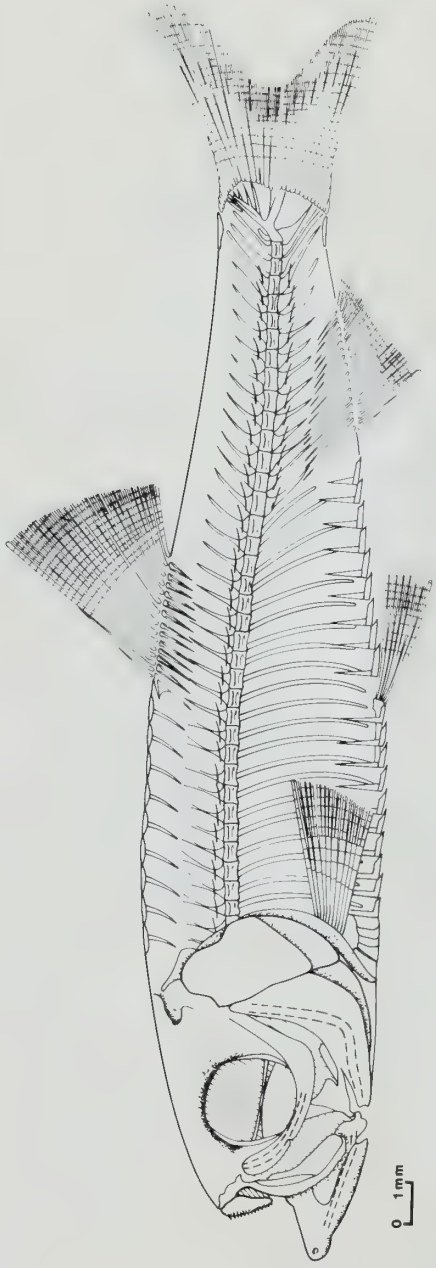

Fig. 12 Reconstruction of *Vectichthys vectensis* (Newton).

more principal dorsal and anal fin rays (respectively 12 and 14–17 against 9–10 and 11) and fewer dorsal scutes (8–9 against 10–13). Anatomical differences can also be noted, as *Gosiutichthys* has small conical teeth on the dentary and a more slender posterior supramaxillary.

On the other hand, Grande (1982*b*) suggests that '*Knightia*' *brasiliensis* Woodward, from the Cenozoic of Maranhão (Brazil), might be congeneric with '*Clupea*' *vectensis* Newton. In the present state of knowledge, this suggestion does not seem to be sufficiently founded, as Grande himself notes that the anatomy of the Brazilian species is still imperfectly known; it is not possible to determine either the shape of its dorsal scutes or the number of supramaxillary bones.

Finally, as demonstrated by Grande (1982*a*), *Ellimma branneri* (Jordan), from the Alagôas series (? Upper Eocene) of Riacho Doce (Brazil), which was considered by Schaeffer (1947) to belong to *Knightia* Jordan, must be left aside in a separate genus as it has two supramaxillaries (Grande 1982*b*: fig. 19) and ornamented dorsal scutes (Grande 1982*a*: fig. 23).

So, if we make reference to the diagnoses of *Knightia* Jordan, *Gosiutichthys* Grande and *Ellimma* Jordan, the double-armoured clupeid from the Isle of Wight does not belong to any of these genera. For this reason, the species initially described as *Clupea vectensis* Newton must be considered the type-species of a new, currently monotypic, genus here named *Vectichthys*, the diagnosis of which is given on p. 22.

It is relatively difficult to determine the precise systematic position of *Vectichthys* within the Clupeidae. According to Grande (1985), five subfamilies may be recognized in this family (Dussumieriinae and Spratelloidinae included). As shown by Grande (1982*a*, 1985), fishes with dorsal scutes are known in most of them. In many species only one dorsal scute is present. But in others, such as *Clupanodon thrissa* (Lacépède) (Dorosomatinae), *Ethmidium maculatum* (Valenciennes) (Alosinae), *Gosiutichthys parvus* (Grande) and *Ellimma branneri* (Jordan) (Clupeinae) and several Pellonulinae (*Hyperlophus*, *Potamolosa* and *Knightia eocaena* Jordan), there is an extended series between the skull and the dorsal fin. Among these forms with many dorsal scutes those of *Vectichthys* appear to match the circular to oval type found in the pellonuline genera. Grande (1982*a*: 30) ranks dorsal scutes of this shape as derived within clupeid fishes and if this is so it may be taken as evidence of pellonuline affinites for *Vectichthys*. The caveat to this view is that a single dorsal scute of similar shape is also found in the clupeines *Herklotsichthys*, *Opisthonema*, *Sardinella* and *Gosiutichthys* (Grande 1982*b*), and in some *Alosa* spp. (Grande 1982*a*).

The Pellonulinae, as characterized by Grande (1985), are recognized by the absence of an anterior supramaxilla, which suggests *Vectichthys* is more plesiomorphic in this respect. Furthermore, the assumed more plesiomorphic pellonulines (*Potamolosa*, *Hyperlophus*, *Clupeoides* and *Sierrathrissa*—Grande 1985: fig. 21) show separate PU1 and U1, like *Vectichthys*. Thus, *Vectichthys* might be considered as the most plesiomorphic pellonuline, showing a continuous series of ovoid dorsal scutes but lacking specializations in the caudal skeleton and the supramaxillary series. *Gosiutichthys* is very similar to *Vectichthys* in these respects but retains two supramaxillary bones and is provisionally considered as a clupeine by Grande (1982*b*).

Order **PERCIFORMES** Bleeker, 1859

Suborder **GOBIOIDEI** Berg, 1940

Family **GOBIIDAE** Bonaparte, 1831

Genus ***POMATOSCHISTUS*** Gill, 1864

Pomatoschistus (?) cf. ***bleicheri*** (Sauvage, 1883)
Figs 13–16

1979 *Gobius*; Ford: 109.

Material. The occurrence of fossil gobiids in the Chapelcorner Fish Bed was reported first by Ford (1979). His collection included one small fish which we were able to identify as a representative of this family, during a short visit to Yarmouth (May, 1977). Several other specimens

(BMNH P.59774–7, P.59784–8 and P.59797) have been collected subsequently at King's Quay. Moreover, two small gobiids have been recognized among the clupeids from the Chapelcorner Fish Bed kept in the Sedgwick Museum (C.23632–3).

DESCRIPTION. The gobiids from the Chapelcorner Fish Bed are small, elongate fishes, the standard length of which does not exceed 35 mm. The height of the body is about one-fifth or one-sixth of standard length. The head is large, its length being included about 3 or $3\frac{1}{2}$ times in the standard length. The caudal fin is rounded and is only one-sixth of standard length. The caudal peduncle is elongate: its length equals about $2\frac{1}{2}$ times its width. The main measurements of the two complete specimens are on file in the Department of Palaeontology, British Museum (Natural History).

P.59786 is a well-preserved small specimen, the head of which is crushed dorsoventrally. Both frontals (Fr) are clearly exposed. Their supraorbital part, which is relatively broad, is delimited laterally by a regularly rounded orbital edge. In front of the frontals, the mesethmoid is partially preserved. The hind part of the skull roof exhibits the supraoccipital, somewhat displaced. The dermopterotic can also be recognized.

In the upper jaw, the premaxillary (Pmx) is large. Its toothed oral process constitutes the entire oral edge of the jaw.

The lower jaw is well exposed on specimen P.59784 (Fig. 14), where its two rami are still in connection. The angular and the dentary can be recognized. Moreover, an isolated dentary is also preserved on slab P.59775. The oral edge is provided with small conical teeth and rises gently backwards before ending in a rounded coronoid process. The quadrate (Q) is triangular and shows a posterior furrow into which fits the symplectic (Sy). Anteriorly, the ectopterygoid (Ecpt) lies in front of the quadrate. It is overlapped by the rod-like entopterygoid (Enpt). The preoperculum (Pop) has two arms, the lower of which is the longer. The operculum (Op) is triangular and has a convex upper edge. It is covered with cycloid scales. Beneath the operculum, the suboperculum (Sop) is relatively narrow.

Of the hyoid arch, the hyomandibular, which has a very massive proximal part, can be seen on specimen C.23632. The symplectic tapers regularly towards the distal end, as shown by P.59784 on which a posterior ceratohyal (Chy 2) is also preserved. This bone has a widened proximal part. It bears six narrow, needle-like branchiostegal rays (R br.).

The vertebral column contains about 30 vertebrae: 12 abdominal and 18 postabdominal. The vertebral centra are elongate and constricted midway along their length. The neural and haemal spines of postabdominal vertebrae are moderately elongate as their distal ends reach only about two-thirds of the distance between the dorsal (or ventral) part of the vertebral centra and the dorsal (or ventral) mid-line of body. The last three postabdominal vertebrae constitute the endoskeleton of the caudal fin with their enlarged haemal and neural spines. The ribs are relatively short and slender and are borne by strong parapophyses, more strongly developed in the hind part of the abdominal region. There are about 10 pairs of ribs.

The margin of the caudal fin is either more or less convex or truncated, as shown by P.59784 in which 12 principal fin-rays, both articulated and branched, can be counted. In front of these about 12 short marginal (procurrent) rays are present, both dorsally and ventrally. The caudal fin rays are supported by three vertebrae: two preural ones (PU_2 and PU_3) and the uro-terminal complex ($PU_1 + U_1$), fused with the triangular dorsal hypural plate (Hy 3 + 4) (Fig. 15). There is a narrow, rod-like upper hypural (Hy 5), while the large triangular lower hypural plate (Hy 1 + 2) articulates with the ventral part of the uro-terminal complex. The parhypural (PHy) originates immediately in front of the lower hypural plate. Dorsally, one epural (Ep) is present. In front of this, the posterior free preural centrum (PU_2) bears a short neurapophysis, while the corresponding haemapophysis is normally developed, as are the apophyses borne by PU_3.

Fig. 13 *Pomatoschistus* (?) cf. *bleicheri* (Sauvage), Chapelcorner Fish Bed, King's Quay, Isle of Wight. A, general view of P.59785 (× 6). B, general view of P.59784 (× 4); see also Figs 14–15. C, head of P.59786 (× 10).

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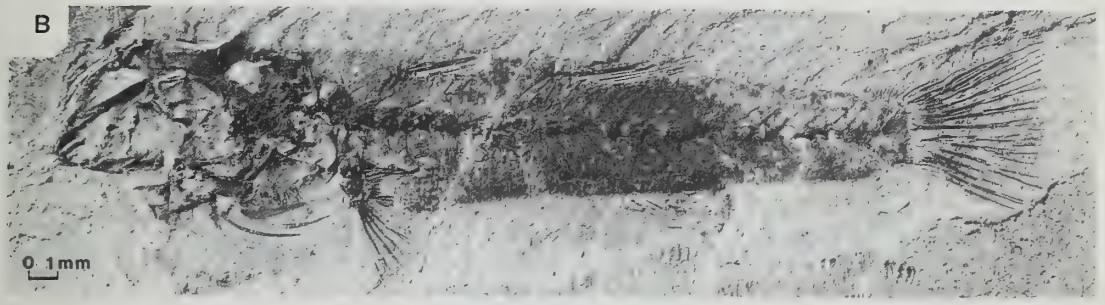
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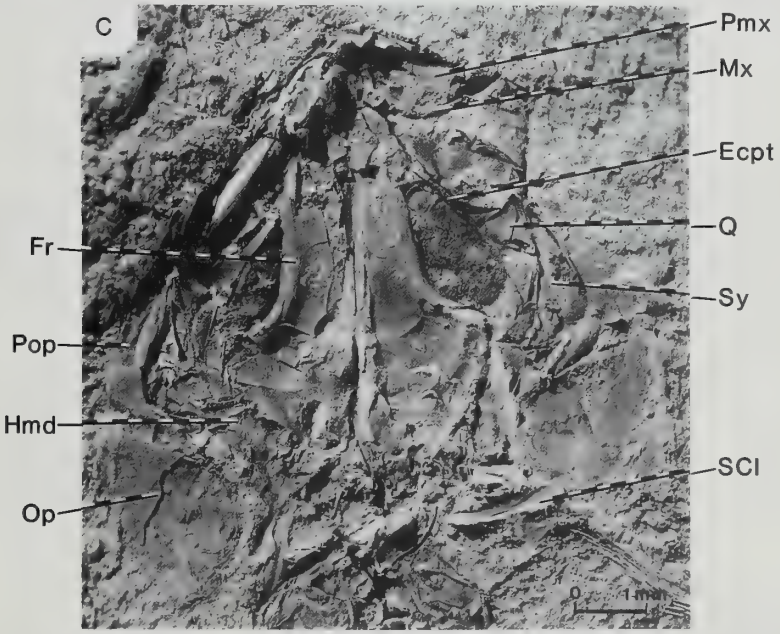
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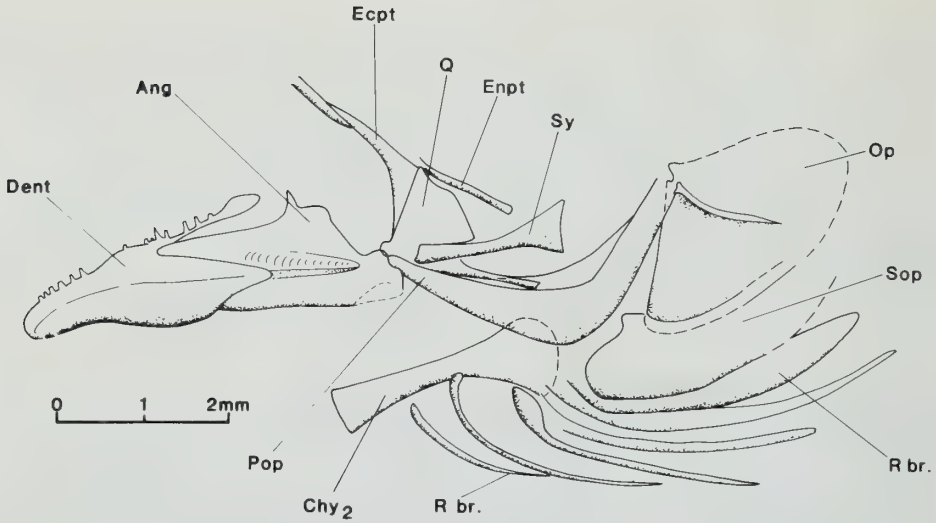

Fig. 14 *Pomatoschistus* (?) cf. *bleicheri* (Sauvage). Partial view of the cheek (P.59784).

The anterior dorsal fin originates in front of the middle of the body. It comprises six or sometimes seven short, slender spines, the distal ends of which do not reach the beginning of the posterior dorsal fin. The second or third spine is the longest; its length equals about two-thirds of the distance between the origin of the two dorsal fins. The endoskeleton of the anterior dorsal fin is composed of six or seven rod-like pterygiophores.

The posterior dorsal fin is situated in the posterior half of the body. It is composed of a short slender spine and nine or ten articulated rays; the first one is unbranched. This ray is the longest of the fin, equal in length to about 0·7 or 0·8 of the maximum height of the body, while the other rays are progressively shorter backwards. The endoskeleton consists of 10 or 11 rod-like pterygiophores.

The anal fin is exactly opposed to the posterior dorsal; it begins precisely under the origin of this fin or slightly behind it. It is composed of one short slender spine and eight or nine articulated rays (of which only the first one is unbranched). The length of the anal fin is slightly less than that of the posterior dorsal. The endoskeleton comprises about 10 pterygiophores.

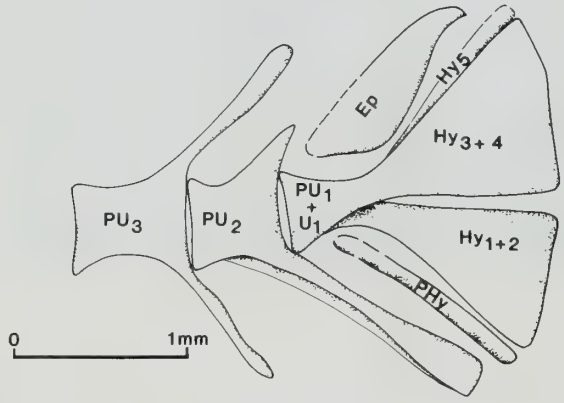

Fig. 15 *Pomatoschistus* (?) cf. *bleicheri* (Sauvage). Axial caudal skeleton (P.59784).

The pectoral girdle remains poorly known. The cleithrum is partly preserved on specimens P.59784–5. An elongate, dorsally tapering supracleithrum is exposed on P.59786, while a forked post-temporal is present on P.59785. The endoskeletal bones of the pectoral girdle are not preserved, although P.59787 shows enlarged radials. The pectoral fins are inserted in the lower third of the flank, and comprise about 14 rays of moderate length.

The pelvic fins are situated just under and slightly in front of the pectorals. They consist of one short slender spine and five rays. It is not known if the pelvic fins were united as in Recent gobiid fishes (*sensu* Regan 1911).

The body as seen in P.59786 is covered with ctenoid scales, the free edge of which is ornamented with a series of small spines. In medial view, the scale surface is covered with a series of longitudinal, more or less winding lines. As pointed out earlier, cycloid scales, showing regularly concentric circuli, are present on the head (especially on the operculum of P.59786).

Relationships. It is always difficult to make precise taxonomic determination of fossil gobiid fishes. In fact, to distinguish Recent genera of this family, ichthyologists use soft anatomical characters of the cephalic sensory system which are, of course, not preserved in fossils. For this reason, it may seem more simple to consider fossil gobiid species as members of the genus *Gobius* L. (s.l.). However, several meristic and morphometric characters of the gobiids described in this paper allow a comparison with the Recent genus *Pomatoschistus* Gill. In fact, the number of vertebrae and the construction of the unpaired fins in the fossil gobiid from the Chapelcorner Fish Bed do not differ significantly from those exhibited by several Recent species of *Pomatoschistus* Gill, especially *P. minutus* (Pallas) and *P. canestrini* (Ninni). For example, it may be noted that, like *P. minutus*, the present fossil gobiid sometimes has seven spines in the anterior dorsal fin. Another character, the occurrence of a long and slender caudal peduncle, also suggests a comparison between it and the Recent species of *Pomatoschistus* Gill.

If these meristic and morphometric characters are sufficient to allocate the Isle of Wight fossil gobiid to the genus *Pomatoschistus* Gill, it still remains to determine its probable relationship to other species belonging to this genus. Among the Recent species, the greatest similarity is to be found with *P. canestrini*, the unpaired fins of which are very similar to those of the fossil gobiid. However, it must be noted that *P. canestrini* (Ninni) never has seven spines in the anterior dorsal fin. This is a feature of *P. minutus* which, otherwise, has 10–12 rays in both the posterior dorsal and the anal fins (Tortonese 1975).

A comparison of the gobiid from the Fish Bed with a fossil species from the Lower Oligocene of Alsace, recently considered as probably belonging to *Pomatoschistus* Gill (Gaudant 1979), shows that no significant difference exists between them. Recently, new specimens of *P. bleicheri* (Sauvage) (first described as *Paralates bleicheri* Sauvage 1883: 485) have been collected from Strangenberg quarry, near Rouffach, which provide more information concerning this species. The diagnosis given earlier (Gaudant 1979) must be slightly emended as the number of post-abdominal vertebrae can be 17 or 18 (not just 17), while the number of soft rays of the posterior dorsal fin is nine or ten (not just ten). These small modifications of the diagnosis of *Pomatoschistus bleicheri* leave no significant meristic or morphometric difference between it and the gobiid in the Chapelcorner Fish Bed. For this reason, we consider that the fossil gobiid from the Isle of Wight may belong to, or is very close to, *P. bleicheri*. However, it must be emphasized that the assignment of this species to the Recent genus *Pomatoschistus* remains provisional, as already noted for the material from Rouffach (Gaudant 1979).

Interpretation of Palaeoenvironment

The fossil content of the grey-bluish shaly clay generally known as the Chapelcorner Fish Bed includes a palaemonid prawn (*Propalaemon osborniensis*) and three fish species: *Amia* (?) sp., *Vectichthys vectensis* and *Pomatoschistus* (?) cf. *bleicheri*. This fossil association and the mode of fossilization of each species are very significant and may be used for determining the conditions of deposition of the Chapelcorner Fish Bed.

Except for the amiid remains, which are exclusively isolated bones and scales, all other fossils collected are articulated skeletons. This could indicate that the amiid remains were washed in

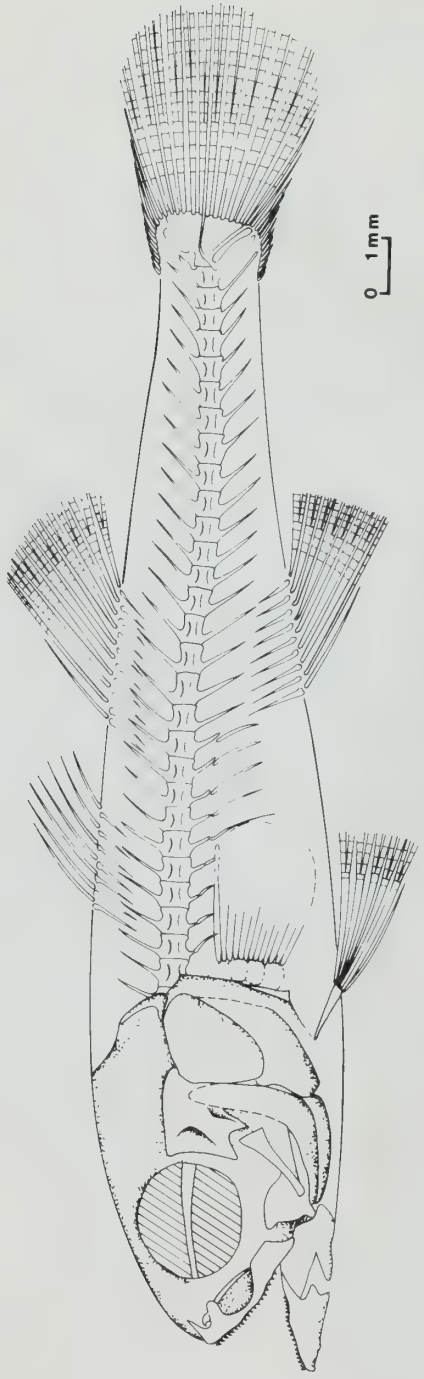

Fig. 16 Reconstruction of *Pomatoschistus* (?) cf. *bleicheri* (Sauvage).

while other animals were living in the area of deposition of the fossiliferous clay. If taken separately, the three animal species here considered as autochthonous do not clearly characterize any precise type of palaeoenvironment. In fact, all belong to euryhaline families, able to live in sea, brackish or fresh water.

Palaemonid prawns belonging to the subfamily Palaemoninae are now living in these three types of environments throughout the world (America, Europe, west Africa, Mediterranean, Indo-Pacific region). For example, the genus *Leander* Desmarest, with about 50 species, is mainly distributed in sea-water but has several fresh-water species, while *Palaemonetes* Heller, with 15 species, lives mainly in estuaries or in brackish water, but is also represented in fresh water. Conversely, *Palaemon* Weber has about 75 species and is mainly fresh-water, although some of them are also present in estuaries (Panikkar 1941). In his extensive study of Recent American Palaemoninae, Holthuis (1952) has shown that these prawns live in every type of aquatic environment (marine, estuarine, lagoonal, fresh-water and even subterranean waters).

Among fossil Cenozoic palaemonids found in Europe and North America, several species ('*Palaemon*' *exul* Frič and *Bechleja inopinata* Houša, from the Oligocene of Kučlín; *Micropsalis papyracea* von Meyer, from the Upper Oligocene of Rott; *Homelys minor* von Meyer, from the Middle Miocene of Öhningen) are considered to have lived in fresh water. The same seems to have been true for the North American species *Bechleja rostrata* Feldmann, Grande & McCoy, recently described in the F 2 unit of the Green River Formation, in which it is associated with fresh-water fishes such as moon-eyes (*Eohiodon falcatus* Grande), gars (*Lepisosteus simplex* (Leidy)) and stingrays (*Heliobatis radians* Marsh).

Recent double-armoured representatives of the subfamily Pellonulinae live exclusively in Australasia (*Hyperlophus* Ogilby and *Potamalosa* Ogilby), where they either inhabit fresh water (*Potamalosa*) or are diadromous (*Hyperlophus*).

The occurrence of a gobiid—tentatively referred to the genus *Pomatoschistus* is no more indicative of the salinity. In fact, although they belong to a primarily marine family, some Recent gobiids are exclusively fresh-water as, for example, the two Italian species *G. nigricans* Canestrini and *Padogobius martensi* (Günther) (Gandolfi & Tongiorgi 1974). Moreover, at least two European species of *Pomatoschistus* (*P. minutus* (Pallas) and *P. canestrini* (Ninni)) are euryhaline. *P. canestrini* has fresh-water populations living in a Jugoslavian river (Ladiges & Vogt 1965).

In conclusion, it is only possible to suggest that the autochthonous fishes and crustaceans found in the 'Chapelcorner Fish Bed' are all more or less euryhaline organisms, which seem to indicate a brackish water palaeoenvironment in which no exclusively marine animal was able to live. The presence of scattered remains of *Amia* may be explained by suggesting that they lived in rivers flooding towards the lagoon in which deposition of the fossiliferous clay took place.

The palaeoclimatic information provided by fossils found in the Chapelcorner Fish Bed is somewhat imprecise. Palaemonid prawns are cosmopolitan and the generic assignment of the gobiids is only provisional. Nevertheless, *Vectichthys* stands very near the Recent 'Hyperlophini' which inhabit Australian waters in which palaemonid prawns also live. This may suggest that during the deposition of the fossiliferous clay the climate was relatively hot and humid, like that of Recent tropical or subtropical regions, as suggested by Daley (1972) for Bembridge Marl times. However, information provided by the fossil content of the Chapelcorner Fish Bed is still too scanty to allow a sound palaeoclimatic interpretation.

Acknowledgements

Grateful thanks are due to Mr J. S. H. Collins, Dr L. Grande, Dr P. L. Forey and Mr S. F. Morris for reading parts of the manuscript and suggesting helpful changes. Mr R. L. E. Ford (Yarmouth) is warmly acknowledged for hospitality and assistance given to the senior author during field work near Wootton Creek (May 1977). For allowing access to material and/or information, we are also indebted to Dr H. W. Ball (BMNH), Dr I. Cooke (British Geological Survey, Keyworth), Mr J. Cooper (BMNH), Dr J. Cooper (Booth Museum of Natural History, Brighton), Dr R. M. C. Eagar (UMMG), Dr G. F. Elliott

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Heterotheca Benson; Lyginopterid pollen organs or coprolites?

G. W. Rothwell[1] and A. C. Scott[2]

[1]Department of Botany, Ohio University, Athens, Ohio 47501, U.S.A.
[2]Geology Department, Royal Holloway and Bedford New College, Egham, Surrey TW20 0EX

Synopsis

A reinvestigation of the originally described specimens of *Heterotheca grievii* Benson, putative pollen organ of the Lower Carboniferous plant *Heterangium grievii*, reveals that all are coprolites.

Introduction

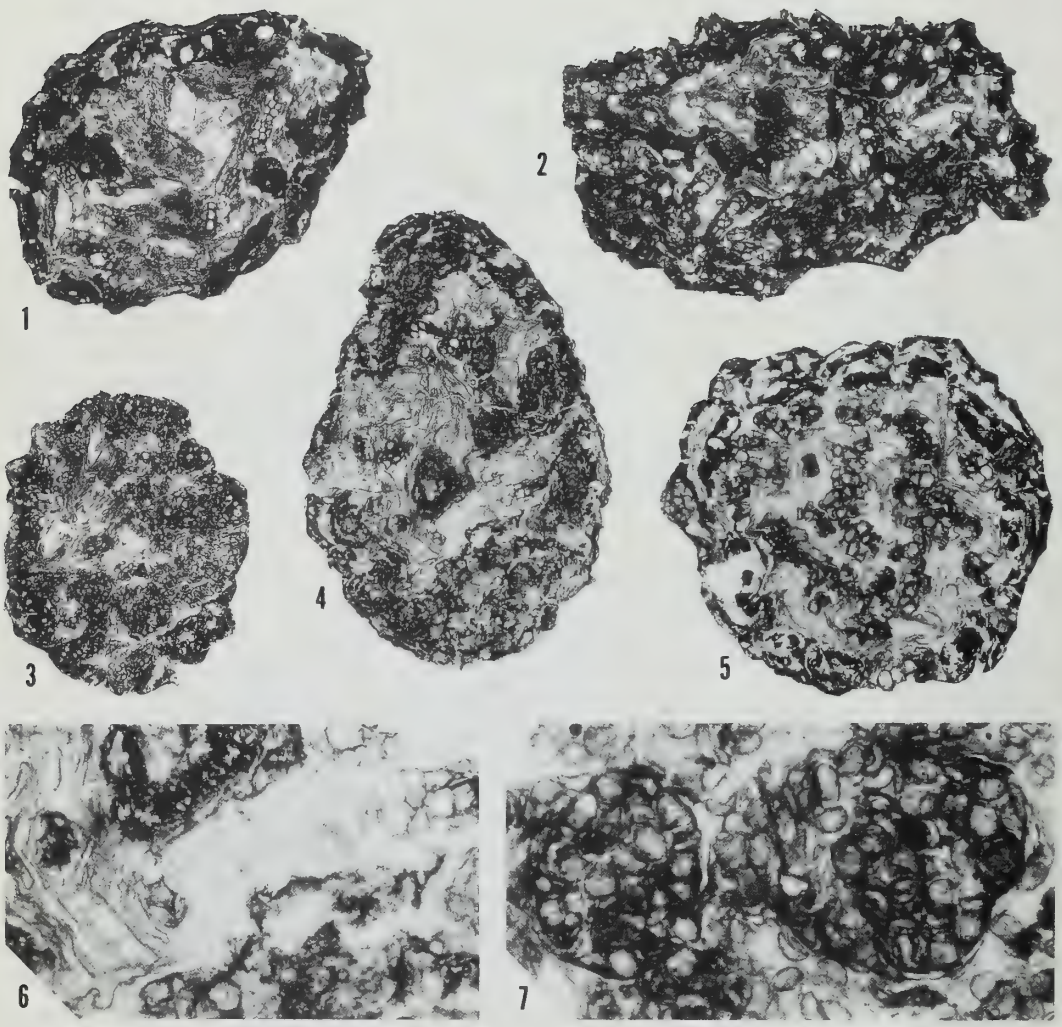
The description of *Heterotheca grievii* Benson (1922) established a record of putative lyginopterid pollen organs in Lower Carboniferous strata, and provided a structural model for interpreting evolution among microsporangiate fructifications of the most primitive gymnosperms (Benson 1922, Schopf 1949). Specimens occur within blocks of permineralized peat collected on the beach near Pettycur, Fifeshire, Scotland (Gordon 1909), and are late Viséan in age (Gordon 1909, Scott *et al.* 1984). Additional specimens of *Heterotheca* have not been reported, but a reconstruction has been offered (Schopf 1949). The generic name has also been changed to *Bensoniotheca* because *Heterotheca* was used earlier for a genus of extant angiosperms (Mickle & Rothwell 1979).

Description and Discussion

Benson described *Heterotheca* from 60 specimens. Twenty-three of these are now housed in the Department of Palaeontology, British Museum (Natural History), and together with new material from Pettycur, are the data upon which this investigation is based. The specimens are irregularly subspheroidal–ellipsoidal, ovoid in cross sections, 1 mm in diameter, and 3·5–4·0 mm long (Figs 1–5). They have an undulating outer surface, and no consistent internal structure or histological features (Figs 1–5). Most specimens consist of heterogeneous fragments of plant tissue (e.g. Fig. 6), but a small number are represented by masses of spores (Figs 3, 7). The spores occur as irregularly-shaped aggregates of variable density, but they are not surrounded by a cellular envelope and do not represent sporangia. At the periphery of many specimens the material is darker than in the center (Figs 1, 2).

Heterotheca conforms to the structure of coprolites that are commonly encountered in Carboniferous and more recent strata (Scott 1977, Baxendale 1979, Rothwell & Scott 1983, Scott & Taylor 1983). From the content of the specimens, it is clear that they were produced by herbivores (phytophagous arthropods), several groups of which were present in the Lower Carboniferous. Of these, *Heterotheca* specimens are most similar to the size range of faecal pellets produced by millipedes (Scott & Taylor 1983). The relatively consistent size and heterogeneous content of the specimens suggests that they represent the faeces of a single type of animal with a relatively nonspecific diet. However, a small number of specimens consist almost entirely of spore exines, and this introduces the possibility that two or more animals of similar size but differing diet may have produced the coprolites.

Heterotheca is the second type of putative seed-fern pollen organ to have been recently recognized as coprolites. The first, *Thuringia callipteroides* Remy, had been attributed originally to Permian callipterid foliage (Meyen 1984). *Heterotheca* and *Thuringia* have both contributed significantly to a misunderstanding about the structure of early seed-fern microsporangia and to the misinterpretation of gymnospermous evolution. This emphasizes the difficulties inherent in characterizing taxa from poorly-preserved specimens where sporangia cannot be separated clearly from faecal pellets containing pollen and spores.



Figs 1–7 Sections of *Heterotheca grievii* coprolites. All specimens housed in the Department of Palaeontology, British Museum (Natural History). Figs 1–2, specimens composed of cellular debris showing irregular shapes, surface features and internal structures: note darker colour of material near periphery of specimens. Fig. 1, slide 387-10 (Specimen C), × 32. Fig. 2, slide 395-6 (Specimen B), × 32. Fig. 3, specimen composed almost entirely of spores; slide 307-18, × 32. Figs 4–5, specimens similar to those in Figs 1–2 except that the peripheral area is not distinctly darker. Fig. 4, slide 387-10, × 50. Fig. 5, slide 386-12, × 50. Fig. 6, enlargement of cellular debris from specimen in Fig. 4; slide 387-10, × 80. Fig. 7, enlargement of sporogenous contents from specimen in Fig. 3; slide 307-18, × 160.

One additional point about our understanding of these fossils concerns nomenclature. The name *Heterotheca* Benson is illegitimate for plant remains because it is a later homonym of *Heterotheca* Cassini (Mickle & Rothwell 1979). However, the recognition that specimens of *Heterotheca* Benson represent coprolites removes the name from consideration under the Botanical Code (Voss *et al.* 1983). The name, however, is also preoccupied in zoology (Stechow 1921: 260), so if it is felt desirable to give these coprolites any 'generic' name as zoological ichnofossils, the replacement name *Bensoniotheca* Mickle & Rothwell (1979) is available for this purpose.

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Mesozoic Neuroptera and Raphidioptera (Insecta) in Britain

P. E. S. Whalley

Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Synopsis

The problems of identification and classification of the Neuroptera and Raphidioptera (Insecta) are discussed. Specimens from the British Mesozoic are reviewed and three new species (*Archeosmylus complexus*, *A. alysius* and *Prohemerobius aldertonensis*) are described. A type species for *Prohemerobius* Handlirsch, 1906, is designated.

Introduction

The present study of Mesozoic Neuroptera and Raphidioptera forms part of a project on the so-called 'Panorpoid complex' in Britain. Tillyard (1918–19) used the term to include the Neuroptera, Mecoptera, Trichoptera, Lepidoptera, Diptera and Siphonaptera. The Neuroptera *sensu* Tillyard included the Orders Megaloptera, Raphidioptera and Neuroptera (Planipennia). These are considered as a monophyletic group, the Neuropteridea (Neuropteroidea *sensu auctt.*), within the Holometabola (Kristensen 1975, Hennig 1981). The remainder of the Panorpoid complex *sensu* Tillyard is now placed in the monophyletic Mecopteroidea (Kristensen 1975). Boudreaux' (1981) emendations, Neuropterida and Panorpida, have not been widely accepted to replace the better-known Neuropteroidea and Mecopteroidea. The Mecopteroidea will be considered in a subsequent publication.

Martynova (1962) recognized three Orders within the Neuropteridea (Neuropteroidea) in her study of fossil insects and this classification is followed in the present paper. Although her work was primarily concerned with fossil insects in the U.S.S.R., she also considered fossil Neuropteridea from the rest of the world.

No comprehensive study of fossil Neuroptera and Raphidioptera in Britain has been made. Brodie (1845) figured a number of insects he considered neuropterous. Although he was the first to figure neuropterous insects from the Mesozoic rocks of Britain he did not provide names for them, describing them as '*Corydalis*' (a Recent genus of Megaloptera) or 'neuropterous insects'. Giebel (1856) provided names for many of Brodie's figures, including some listed as neuropterous, and these species were subsequently re-evaluated by Handlirsch (1906).

Table 1 gives the specimens figured by Brodie (1845) and Westwood (1854) as 'neuropterous insects' or '*Corydalis*' and indicates their current taxonomic position. All the specimens are in the collection of the British Museum (Natural History) unless otherwise stated.

Scudder (1886) described two fossil wings as Blattodea which Handlirsch (1906) recognized as Neuroptera.

Tillyard (1933) described two species of Neuroptera from the Lower Lias of Britain. He associated the Neuroptera *sensu stricto* with the Mecoptera and other orders of insects in the Panorpoid Complex although he expressed some reservation about this. He suggested that they were linked 'somewhat loosely with the Mecoptera through the ancient suborder Protomecoptera'. Nevertheless he went on to consider the Neuroptera as the 'most Primitive members of the Complex, and appear with the Mecoptera in the Lower Permian' (Tillyard 1933: 8). Kristensen (1975) pointed out that this association was based on the general phenetic resemblance of the more primitive members of the two orders, neither of which has greatly differentiated from their ancestral holometabolan type. No evidence has yet been presented of any synapomorphies from these orders which cannot, therefore, be considered to have a common ancestor separate from other Holometabola. Hennig (1981) considered that there was good

Table 1 Current systematic position of fossil insects described as 'neuropterous' or '*Corydalis*' by Brodie, 1845 and Westwood, 1854. (*Brodie (1845: 102) probably made a mistake in referring to fig. 15 (dragonfly abdomen) when he should have said fig. 16. Tillyard (1933: 64) synonymized *H. higginsi* with *Necrotaulius furcatus* Giebel on the basis that Brodie's references to figs 15 and 16 were mixed. A type designation for this species will be given in a subsequent publication on the Mecoptera.)

Plate number	Figure	Brodie's name (1845)	Current systematic position
5	2	*Corydalis*	Blattodea, *Nanoblattina similis* (Giebel)
5	3	*Corydalis*	Blattodea
5	12	Neuropterous (cf. *Orthophlebia*)	Mecoptera, *Orthophlebia bifurcata* (Giebel)
5	13	*Corydalis*	Orthoptera, *Zalamona brodiei* Giebel
5	14	*Corydalis*	Blattodea, *Blatta kollari* Giebel
5	16	*Corydalis*	Blattodea, *Nanoblattina brodiei* (Giebel)
5	18	Neuropterous (cf. *Orthophlebia*)	Mecoptera, *Stenopanorpa gracilis* (Giebel)
5	21	Neuropterous (cf. *Orthophlebia*)	Orthoptera, [*Bittacus dubius* Giebel][1]
6	22	*Hemerobius gigantea* Buckland	Odonata, *Isophlebia gigantea* (Buckland) (Handlirsch, 1906: 583)
8	10	Neuropterous	Hemiptera–Homoptera
8	11	Neuropterous	Orthoptera
8	16	Neuropterous	Odonata
9	15	*Hemerobius higginsi* (p. 102) (See * above)	
9	15	'abdomen of dragonfly' (p. 126) (See * above)	
9	16	Neuropterous (cf. *Panorpa*)	Mecoptera, *Necrotaulius furcatus* (Giebel)
9	17	Neuropterous (cf. *Panorpa*)	Mecoptera, *Necrotaulius liasina* (Giebel)
Plate number	**Figure**	**Westwood's name (1854)**	**Current systematic position**
15	16	*Termitidium ignotum*	Probably Orthoptera[2]
17	12	*Panorpidium tessellatum* var.	Probably Orthoptera[2]
18	24	*Sialium sipylus*	Nymphitidae[3]
18	39	*Agrionidium aetna*	Probably Orthoptera

[1] Giebel described this as a Mecopteran but it is Orthopterous.
[2] Specimens not examined.
[3] Specimen not examined. The marginal branching is more reminiscent of Neuroptera but from the figure little further can be determined.

evidence for believing that the Coleoptera (+ Strepsiptera) were more closely related to the Neuropteridea (Neuropteroidea) but he also suggested an alternative, that the Mecoptera and Neuroptera could be sister-groups. There is still no concensus on this.

The most primitive holometabolous insects occur in the Neuropteridea (Kristensen 1975) but the relationship of the three orders within the Neuropteridea (Neuroptera, Megaloptera, Raphidioptera) has not yet been resolved (Achtelig & Kristensen 1973).

In studying the neuropterous fossils, all the evidence for their identification is based on wing venation: very few bodies of neuropterous insects have been described. This creates a problem when detailed comparisons of fossil and Recent Neuropteridea are required. In the latter, although the venation of the wings is used in their major classification, other parts of the anatomy are extensively used both for this and the generic and specific classification. While a

general comparison of fossil and Recent wings can be made, the results may not always be significant. This is partly owing to the similarity of the wing venation in many Recent species which may currently be placed in different genera or even different families, and partly to the apparent lack of derived ground-plan characters in the wing.

The identification of a fossil wing as neuropterous is rarely difficult, although fragments have been described as cockroaches (Scudder 1886), but further identification is impeded by the limited number of taxonomic and classificatory characters in the wing venation. The recognition of the fossil as neuropterous is usually, in the first instance, based on the presence of a number of parallel branches of the radial sector (a condition also found in Orthoptera) and the presence of small end-branches ('apical twigging') at the wing margin. These first impressions can be confirmed on closer examination by the presence of trichosors (small structures on the wing margin between the veins). However, trichosors are not easily seen in fossils (and are absent in some Recent Neuroptera), but the presence of numerous subcostal veinlets will also help to confirm the identification.

The classification of the Neuropteridea into Neuroptera, Raphidioptera and Megaloptera, adopted by Martynova (1962), is followed here. There are two families in the Megaloptera. In the Sialidae there are three species in the Recent fauna in Britain but sialids have not been recognized in the British Mesozoic. The other family, Corydalidae, is known only from the New World and has not been found in the fossil record in Britain. The Permosialidae, listed by Martynova (1962) in the Megaloptera, are now considered to belong to Miomoptera.

Two species of Raphidioptera were recently described from the Dorset Lias (Whalley 1985) and there are four living species in Britain. The fossil species were placed in extinct families.

Martynova (1962) divided the Neuroptera into four superfamilies, Myrmeleontoidea, Polystoechotoidea, Hemerobioidea and Coniopterygoidea. (The spelling of these names has been emended from Martynova, 1962, to make the endings agree with the recommendations of the International Code for Zoological Nomenclature.) She defined these superfamilies on the basis of the characters given below and these are used in the current work to identify the British specimens. Because the definitions are based solely on the wings there is some overlap of characters between the genera listed by Martynova in the different groups. For example, the Berothidae (Hemerobioidea) have the subcostal and radial veins joined in many species (Tjeder 1969). Martynova considered that this was due to a cross-vein and that the subcostal vein does actually continue to the wing margin. While this may be true, it is rarely possible to decide from a study of the fossil whether the subcostal and radial veins are joined only by a cross-vein near the apex or whether they actually fuse, with the subcostal curving down to join the radial vein. Although there may be doubt over the interpretation of the origins of the apical anastamosis of the subcostal and radial, in the present study an anastamosis between the subcostal and radial veins (unless clearly due to a cross-vein) is used to make the primary taxonomic division to contrast with those where the subcostal and radial veins can be traced separately to the wing margin. All the specimens where the subcostal and radial can be traced separately to the outer wing margin are placed in the Hemerobioidea; the other specimens, where the subcostal and radial join, are placed in one of the two remaining groups (Myrmeleontoidea, Polystoechotoidea, *sensu* Martynova, 1962).

Distribution and abundance of the fossils

Over 50 Mesozoic sites are currently known in Britain from which insect fossils have been found but fewer than ten of these have yielded any Neuropteridea. Neuroptera are recorded from the Permian (Martynova 1962) but are known only from the Upper Triassic to Lower Cretaceous in the British Mesozoic. Of the Recent families only the Coniopterygidae, Berothidae and Psychopsidae are known from the Mesozoic and few of these occur earlier than the Lower Cretaceous (Whalley 1980).

Fewer than 50 specimens, representing 11 species of Neuropteridea, are known from the British Mesozoic, a period of about 180 million years. Although relatively few specimens are known it is probably significant that these fossils represent eight families, only one of which is

extant. This compares with seven extant families of Neuropteridea in the British fauna and 20 extant families world-wide. In spite of the small numbers the data suggest that there was considerable diversity in Mesozoic Neuropteridea, although this diversity must be considered against the time-scale involved when making a comparison with the Recent fauna.

Fossil Neuropteridea are not common compared with some other insect orders. This either reflects their true status (i.e. they were actually less common), or they were living in areas where they had even less chance of being fossilized. There is no indication of a proportional change in abundance compared with Recent insects which can be seen in, for example, the Mecoptera which were more diverse and abundant in the Mesozoic than in the Recent fauna. Although Neuroptera are delicate insects, they are no more delicate than many of the other insects that were preserved in Mesozoic deposits. In an analysis of the various insect orders in four localities of early and late Jurassic age in Europe and Asia, Whalley (1985) quoted figures to show that Neuropteridea represent less than 7% of the total insect fauna at each of the four sites. Recent Neuroptera tend to be more numerous in woodlands but, being predatory insects, they are never as abundant as phytophagous insects.

In the British Mesozoic Neuropteridea it is evident that only one of the Lower Cretaceous specimens can be referred to a Recent family, the Psychopsidae (Jarzembowski 1984). However, by the Palaeocene (Tertiary) the Recent families Mantispidae (no longer occurring in Britain), Hemerobiidae, Chrysopidae and Sisyridae were all represented in the British fauna (Jarzembowski 1980).

Check list of British Mesozoic Neuropteridea

NEUROPTERA

Polystoechotoidea:

Permithonidae	*Archeosmylus complexus* sp. nov. (p. 50)
	Archeosmylus alysius sp. nov. (p. 50)
Mesopolystoechotidae	*Megapolystoechus magnificus* Tillyard

Hemerobioidea:

Brongniartiellidae	*Actinophlebia intermixta* (Scudder)
	Pterinoblattina pluma (Giebel)
	Pterinoblattina penna (Giebel)
Kalligrammatidae	*Paractinophlebia curtisii* (Scudder)
Prohemerobiidae	*Prohemerobius aldertonensis* sp. nov. (p. 60)
Psychopsidae	(figured in Jarzembowski, 1984: fig. 32)

RAPHIDIOPTERA

Mesoraphidiidae	*Metaraphidia confusa* Whalley 1985
	Mesoraphidia species
Baissopteridae	*Priscaenigma obtusa* Whalley 1985

MEGALOPTERA

No fossil record in Britain; not present in the Recent British fauna.

Subdivisions of the Neuroptera

The following list (after Martynova, 1962) includes all families currently recognized. (*Includes living species).

Coniopterygoidea. Very small insects. Venation very reduced from basic neuropterous plan, without additional marginal forks. Jurassic–Recent. Family Coniopterygidae*. Not known as fossils in Britain although occurring elsewhere in the Mesozoic (Whalley 1980). There are a number of Recent species in Britain.

Myrmeleontoidea. Long, narrow wings; distal part of Sc and R join; anterior branches of M merge with R; MP and Cu1 almost parallel; proximal branches of CuA thicker than the rest of the branches; CuP short. Jurassic–Recent. Families Ascalaphidae*, Myodactylidae*, Myrmeleontidae*, Nemopteridae*, Nymphidae*, Nymphitidae, Solenoptilidae. No Recent species in Britain.

Polystoechotoidea. Forewings more than twice as long as wide; Sc and R joined; MA usually many-branched, merging with Rs near base; MP with two branches; CuA and CuP long, with short, backward-directed, branches; anal veins often stepped. Permian–Recent. Families Archeosmylidae, Ithonidae*. Mesopolystoechotidae, Neurorthidae*, Osmylidae*, Osmylitidae, Permithonidae. One Recent species in Britain.

Hemerobioidea. Wings comparatively wide; Sc not merging with R; Sc, R and Rs approach (except in Chrysopidae, Mesochrysopidae); parallel Sc and R areas together narrower in width than costal area (except Chrysopidae); MA often joins R or Rs. Permian–Recent. Families Berothidae*, Brongniartiellidae, Chrysopidae*, Dilaridae*, Eomantispidae, Hemerobiidae*, Kalligrammatidae, Mantispidae*, Mesochrysopidae, Osmylopsychopidae, Palaemerobiidae, Proberothidae, Prohemerobiidae, Psychopsidae*, Rapismatidae*, Sialidopseidae, Sisyridae*. Recent species in the Hemerobiidae, Sisyridae and Chrysopidae occur in Britain.

Myrmeleontoidea do not occur in the Recent fauna and have yet to be found in the fossil record in Britain. British specimens with Sc and R joined have relatively short, broad wings and are all placed in the superfamily Polystoechotoidea.

Systematics

All numbers given are British Museum (Natural History) register numbers unless otherwise stated.

Order **NEUROPTERA**, lacewings

Superfamily **POLYSTOECHOTOIDEA**

Family **PERMITHONIDAE** Tillyard, 1922

1922 Permithonidae Tillyard: 289.
1953 Archeosmylidae Riek: 85; syn. nov.

Diagnosis. Sc fused at two-thirds from wing-base or nearer centre of wing. Pterostigma long, often running round apex of wing. Radial area wider than subcostal. M branches towards centre of basal half of wing in some species. Rs with 7–10 branches. MA frequently well-branched. CuP simple or with short forks. Cross-veins not in even rows. Permian–Jurassic. (After Martynova, 1962, modified from Riek, 1955.)

Discussion. The similarity between the Permithonidae and Archeosmylidae was mentioned by Martynova (1962) but she did not synonymize them. The separation of the Permithonidae from the Osmylitidae is based on the width of the radial area (radial field of Martynova, 1962) and from the Mesopolystoechotidae by the wing shape (figured in Martynova, 1962). The arrangement of the veins in *Osmylus* and some other genera in the Osmylidae, as in the Polystoechotidae, with cross-veins in the centre of the wing and a broad margin with only longitudinal veins, is used as a guide to these families. Most of the genera in the Permithonidae were from the Permian, but with the synonymizing of Riek's Triassic family the range is now extended. There are insufficient data on the British specimens to create a new genus for them and they are provisionally placed in *Archeosmylus*.

Genus ***ARCHEOSMYLUS*** Riek, 1953

1953 *Archeosmylus* Riek: 86.

Type species. *Archeosmylus pectinatus* Riek (1953: 86), by original designation.

DIAGNOSIS. Sc and R fused. Pterostigma long, curved round apex. Rs with 7–10 branches. Rs and MA fused for a short distance. CuA deeply forked. Anals simple except for marginal branches (after Riek, 1955: 677). Triassic, Australia; Jurassic, U.K.

Archeosmylus complexus sp. nov.
Figs 1, 3

DIAGNOSIS. As genus: each branch of the posterior radial sector divides well before the wing margin.

NAME. 'Complicated'.

DESCRIPTION. Sc and R join one-third from wing apex. Rs with 10 branches, posterior ones divide one-third from wing margin. Trichosors present. Broad subcostal area with numerous veinlets, many branched, R curves down below wing margin towards apex. Rs bifurcated at apex, 10 branches roughly parallel from Rs to wing margin; anterior branches simple, posterior ones branched one-third from margin with short marginal forks. Base of wing missing, MA and MP separate near base but may join together with base of R (area indistinct). Cu incomplete. Anal veins distinct. Few cross-veins preserved though some traces of them present.

MATERIAL. **Holotype**: I.11412, near Dumbleton, Gloucestershire; Brodie colln, 1896. Upper Lias. Dimensions: 9 × 4·5 mm; estimated wing length 9·5–10 mm. Paratype: I.3315, Alderton Hill, Gloucestershire; Slatter colln, 1898. Upper Lias. Other material: I.64664, Wainlode, Gloucestershire; Jarzembowski colln, 1984. Upper Trias.

DISCUSSION. This species has a broad costal area with long parallel veinlets. It is separated from *A. alysius* sp. nov. (below) by its size and by division of the branches of the posterior radial sector. There are other broadly similar species which have been described in the Proberothidae by Riek but these have series of well-preserved cross-veins. *A. complexus* resembles *A. stigmaticus* Riek (1955) from the Triassic of Australia, but the latter had only 9 branches from the radial sector. However, the poor state of preservation is such that a close comparison between these species is not practicable.

The diagnoses given by Riek and Martynova can be applied to a number of similar but probably unrelated fossils, particularly when the specimens are incomplete. The specimen from Wainlode is only provisionally placed here; it shows two overlying wings of the correct size for this species but the details of the costal, subcostal and radial areas are obscure.

Archeosmylus alysius sp. nov.
Figs 2, 4

DIAGNOSIS. As genus. Sc and R join one-third from apex of wing. Rs with 7–8 branches. Most branches of Rs with only small apical forks.

NAME. Arbitrary combination of letters.

DESCRIPTION. Costal margin with numerous veinlets. Trichosors present. R curves round below wing apex. Rs with 7–8 branches, with only small apical branches on wing margin. MP arises near base of MA; latter has two long branches. Cu with several branches. Head flattened anteriorly, broader than long. Head, prothorax and abdomen and part of hindwing preserved but with few details.

MATERIAL. **Holotype**: I.3318, Alderton Hill, Gloucestershire; Slatter colln, 1896. Upper Lias, part and counterpart. Dimensions: wing 4·3 mm (incomplete, estimated 5–5·5 mm). Head to tip of abdomen, 3 mm. Abdomen 2·5 mm. Paratypes: I.11416, near Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias. I.11433, same data. Other material (incomplete, tentatively placed in this species): I.11281, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. I.11375, Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias. I.11402, same data.

DISCUSSION. One of the additional specimens has two overlying wings plus an impression of the shape of the head and thorax, but few details are preserved. All the specimens have a wing

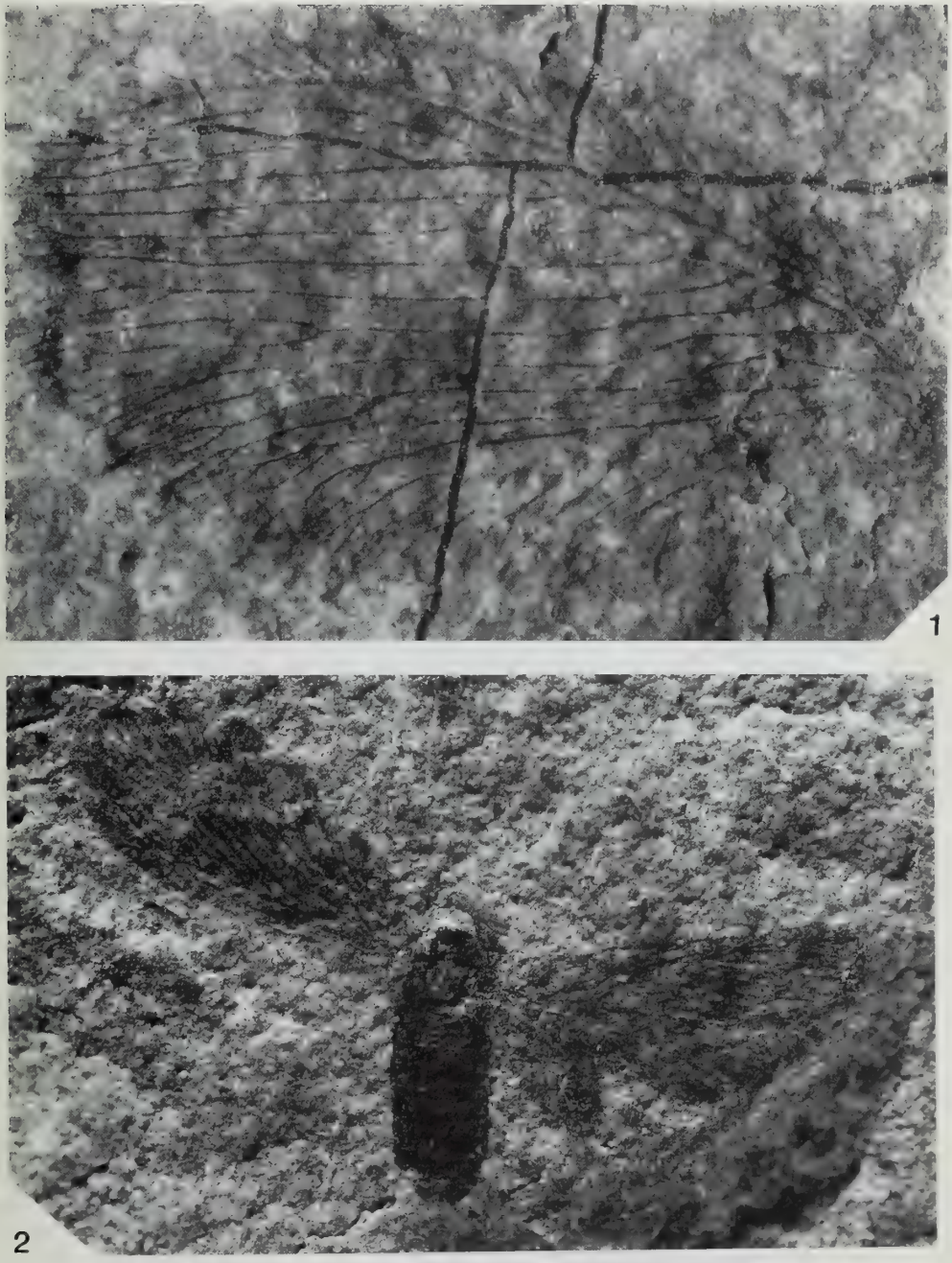


Fig. 1 *Archeosmylus complexus* sp. nov. **Holotype**, I.11412. Upper Lias, Gloucestershire (9 mm).
Fig. 2 *Archeosmylus alysius* sp. nov. **Holotype**, I.3318. Upper Lias, Gloucestershire (4·3 mm).

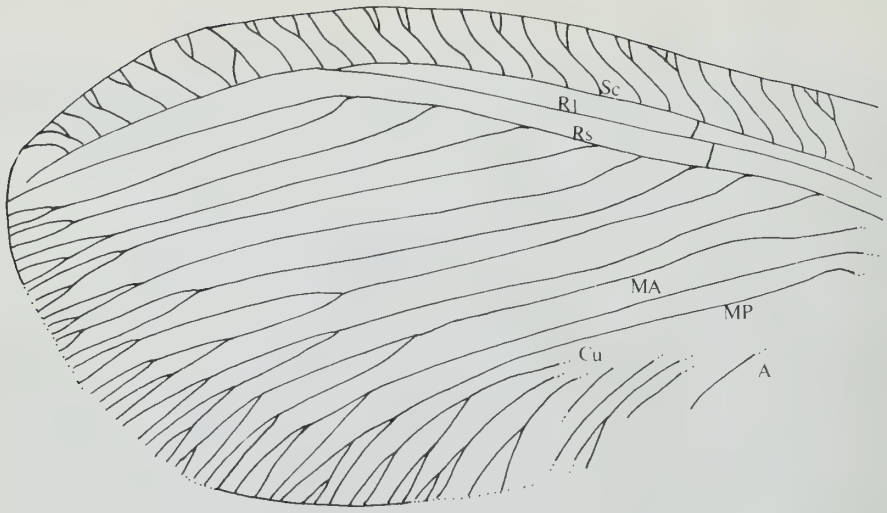


Fig. 3 *Archeosmylus complexus* sp. nov. Venation. A—Anal veins, Cu—Cubital vein, MA—Anterior medial, MP—Post medial, Sc—Subcostal, R1—First radial, Rs—Radial sector.

length of 4–5 mm (wingspan estimated 9–11 mm) and are smaller than the other neuropterous insects from the Mesozoic. Generally the branches from the radial sector remain unbranched themselves until they reach the margin where there are short marginal forks.

I.11281 has the base of the wing overlaid by a fragment of (?) hindwing. This effectively hides the subcostal vein towards the base and makes the specimen look very like a Recent species of *Hemerobius*. However, the base of the costal area of the wing has finely preserved hairs, unlike any of the other specimens, and there appears to be a change in the texture between the outer part of the wing with veinlets and the basal part of the costal area. Thus I think that the subcostal vein was probably present in this specimen, but is obscured. It is provisionally placed in *A. alysius* on the remaining characters and size of the wing.

Family **MESOPOLYSTOECHOTIDAE** Martynova, 1962

DIAGNOSIS. Apex of forewing tending to a point. Sc and R1 gradually merging. Branches of Rs without long forks. MP with two branches (Martynova 1962). Upper Triassic–Jurassic, Europe, Asia.

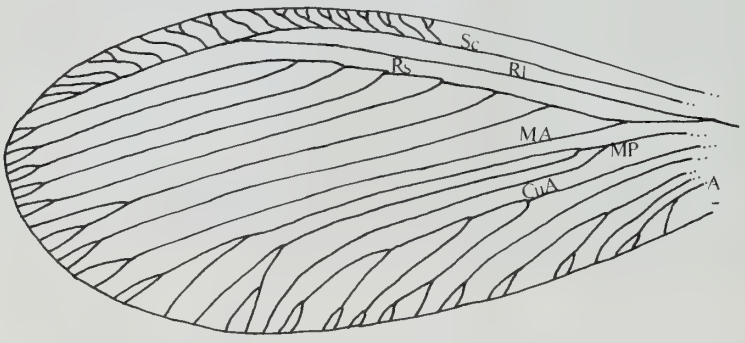


Fig. 4 *Archeosmylus alysius* sp. nov. Venation. A—Anal, CuA—Anterior cubital, MA—Anterior medial, MP—Post medial, Sc—Subcostal, R1—First radial, Rs—Radial sector.

DISCUSSION. This family was erected for the genus *Mesopolystoechus* Martynov, 1937, from the Lower Jurassic of central Asia.

Genus **MEGAPOLYSTOECHUS** Tillyard, 1933

1933 *Megapolystoechus* Tillyard: 12, fig. 1.
1962 *Megapolystoechus* Tillyard; Martynova: 262 (Hemerobiidea, *incertae sedis*).

TYPE SPECIES. *Megapolystoechus magnificus* Tillyard, 1933, by original designation.

DIAGNOSIS. Sc and R merge gradually towards the apex of the wing. Branches of Rs without

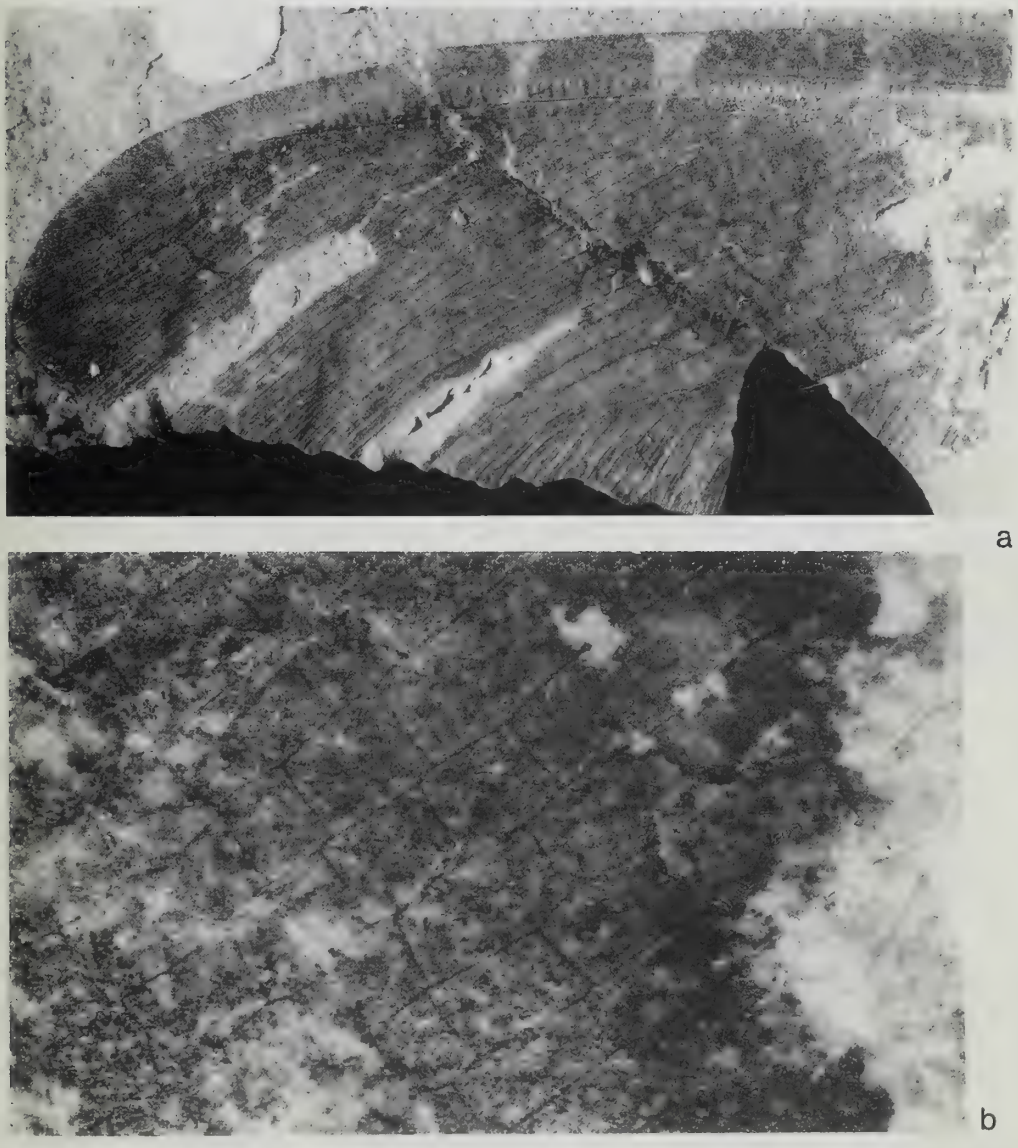


Fig. 5 *Megapolystoechus magnificus* Tillyard. Holotype, I.11027. Upper Trias, Worcestershire (30 mm). a, whole wing. b, wing, details of median and cubital areas.

long forks, Rs with numerous (at least 24) parallel branches. Many cross-veins on the branches of Rs, especially towards the centre of the wing.

DISCUSSION. In the original description and figure of the single species in this genus, Tillyard indicated that the subcostal and radial veins ran separately to the apex of the wing. Re-examination of the type specimen shows that only R runs to the wing apex while Sc curves towards R, joining it before the apex of the wing.

Tillyard's original description contained a number of other errors, apart from his interpretation of the anterior veins; see discussion below. The membrane was very wrinkled and on preservation these wrinkles gave the impression of many cross-veins, especially in the subcostal area; this area and the radial area have in reality nothing like as many cross-veins as indicated by Tillyard (1933: fig. 1). The subcostal area may not have had more than one or two cross-veins but the incomplete preservation makes interpretation difficult: the radial area may have had two or three cross-veins, possibly a few more, but not the 30–40 indicated by Tillyard. Upper Triassic–Upper Lias, U.K.

Megapolystoechus magnificus Tillyard, 1933
Figs 5a, 5b, 6

1933 *M. magnificus* Tillyard: 12.

DIAGNOSIS. As genus.

DESCRIPTION. Incomplete forewing, membrane dark. Branches of Rs may divide several times with narrow, U-shaped, branches to wing margin. R curves round below wing apex. Branches of Rs virtually parallel. Cross-veins preserved near centre of wing, not stepped. Subcostal and radial areas together equal in width to costal area.

MATERIAL. Holotype: I.11027, Strensham, Worcestershire; Brodie colln, 1898. Upper Trias. Paratype: I.10523, data as holotype. Other material: 1983/755, Aust, Gloucestershire; in Yorkshire Museum. Upper Trias.

DISCUSSION. The specimen illustrated by Tillyard (1933: fig. 1) is the holotype (I.11027), not the paratype (I.10523) as indicated in the caption. With the reinterpretation of the holotype it is possible to compare the genus with *Mesopolystoechus* Martynov, from which it differs in the number of cross-veins. There are two gradate series in *Mesopolystoechus* but these are alternately arranged, and more numerous, in *Megapolystoechus*.

Tillyard's estimated wing length of 37 mm may have been rather conservative and it could well have been 40 mm or more.

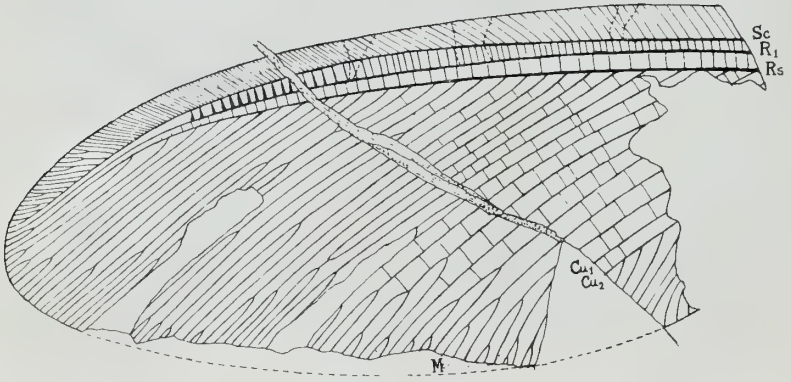


Fig. 6 *Megapolystoechus magnificus* Tillyard. Venation, from Tillyard, 1933: fig. 1.

Superfamily **HEMEROBIOIDEA**, brown lacewings

In all the remaining species the subcostal and radial veins run separately to the wing margin. There are 13 families (Martynova 1962) in the superfamily, ranging widely in size and shape. In Britain, examples of the families Brongniartiellidae, Kalligrammatidae and Psychopsidae have been found in the Lower Cretaceous (Wealden) deposits (Jarzembowski 1984). The superfamily is known from the Permian onwards and includes many living species.

Family **BRONGNIARTIELLIDAE** Martynova, 1949

Diagnosis. Forewing with 12–16 branches to Rs. Wings roughly triangular. MP divides at base of wing, CuA and CuP often with many branches. Few cross-veins (Martynova 1962). Jurassic, Europe.

Discussion. This family, together with the Psychopsidae and Kalligrammatidae, includes species where the relatively large wing size has resulted in an increased number of veins. The possession of large numbers of veins is generally considered a primitive feature (e.g. Imms 1970), presumably because many of the earliest known insects in the Carboniferous had many veins. It is difficult to see how the complicated venation in the three families mentioned above can be derived from the early Permian Neuroptera, or even from the Carboniferous insects, without considering it a specialization, since the venation is not based on the more typical reticulate venation of many Carboniferous insects. Presumably the more complicated venation of these large Neuroptera can be considered as an adaptation of the basic neuropterous venation plan to the structural needs of larger-sized wings.

Genus *ACTINOPHLEBIA* Handlirsch, 1906

1906 *Actinophlebia* Handlirsch: 476.

Type species. *Pterinoblattina megapolitana* Geinitz, by monotypy.

Diagnosis. Forewing subtriangular with numerous costal veinlets. Sc, R and Rs close together, particularly below the pterostigma but running separately to the apex of the wing. Rs with 12–16 branches. Jurassic, Europe.

Discussion. Martynova (1962) transferred this genus to the Brongniartiellidae from the Prohemerobiidae where it had been placed by Handlirsch.

Actinophlebia intermixta (Scudder 1885)
Figs 7, 8

1885 *Pterinoblattina intermixta* Scudder: 107.
1886 *Pterinoblattina intermixta* Scudder; Scudder: 471; pl. 48, fig. 9.
1890 *Pterinoblattina intermixta* Scudder; Scudder: 363; pl. 22, fig. 9.
1906 *Actinophlebia intermixta* (Scudder) Handlirsch: 476.
1933 *Actinophlebia anglicana* Tillyard: 14, fig. 2 (syn. n.).
1939 *Actinophlebia intermedia* (*sic*) (Scudder); Handlirsch: 75.

Diagnosis. As type species of the genus, but smaller and with straight terminal wing margin and sigmoidally waved vein Cu (Tillyard 1933: 15).

Description. Forewing, Sc and R run close together along most of the wing but do not join. Many costal veinlets branched. Anal veins run parallel to hind margin for the first part of the length, ending with short branches on the hind margin. Both Rs and M have many branches.

Material. Holotype (of *intermixta*): I.3577, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. Dimensions: forewing, 11–12 mm × 5·5 mm. Other material: I.11346, near Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias (holotype, *anglicana*). I.11319 and I.1134, Dumbleton, Gloucestershire; Brodie colln, 1898. Upper Lias (paratypes, *anglicana*).

Discussion. Scudder originally described *A. intermixta* as a cockroach but its neuropterous affinities were recognized by Handlirsch (1906). The outer (terminal) margin of the forewing

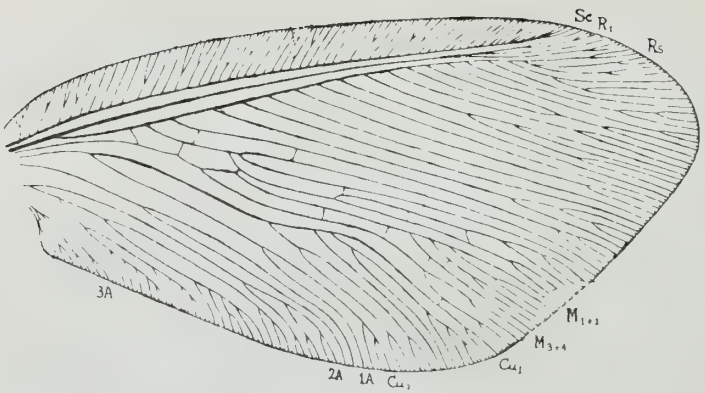


Fig. 7 *Actinophlebia intermixta* (Scudder). Venation, from Tillyard, 1933: fig. 2 (illustrated as *A. anglicana* Tillyard).

subtends an obtuse angle with the hind margin of the wing, which tends to have a pointed apex. Some trichosors are present in all the specimens but are not clearly visible all round the wing. The hindwing and the rest of the body are unknown.

Genus ***PTERINOBLATTINA*** Scudder, 1885

1885 *Pterinoblattina* Scudder: 105.
1886 *Pterinoblattina* Scudder: 486; pl. 22, fig. 7.
1890 *Pterinoblattina* Scudder: 360.
1906 *Pterinoblattina* Scudder; Handlirsch: 607.
1962 *Pterinoblattina* Scudder; Martynova: 279.

Type species. *Pterinoblatinna pluma* (Giebel), by subsequent designation by Handlirsch, 1906: 607.

Discussion. *Pterinoblattina* was described by Scudder as a genus of Blattodea (cockroaches) but was transferred to the Neuroptera by Handlirsch (1906). This was followed by Martynova (1962) who placed the genus in the family Brongniartiellidae. Scudder's figure of the type species (1886: pl. 22, fig. 7) is accurate and examination of the specimen shows that the subcostal runs close to the first radial vein, particularly towards the apex of the wing, but then appears to stop and cannot be traced further forwards. It is probable that it curves down slightly but it does not appear to fuse with the radial vein. From the evidence available the genus is best left in the Brongniartiellidae.

Pterinoblattina pluma (Giebel 1856)
Fig. 9

1854 (unnamed) Westwood: 394; pl. 15, fig. 14.
1856 *Blatta pluma* Giebel: 322.
1885 *Pterinoblattina pluma* (Giebel) Scudder: 105.
1886 *Pterinoblattina pluma* (Giebel); Scudder: 469; pl. 48, figs 7, 8.
1890 *Pterinoblattina pluma* (Giebel); Scudder: 361; pl. 22, figs 7, 8.
1906 *Pterinoblattina pluma* (Giebel); Handlirsch: 607.

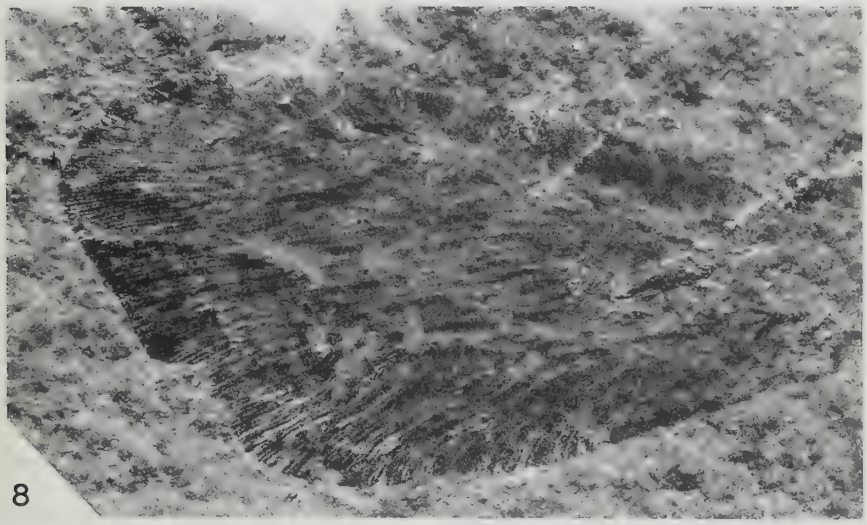
Diagnosis. Sc ends abruptly, probably not joining R. Rs with 8–10 branches, each branch dividing either near or before the centre of the wing, producing some 20–30 marginal branches. Broad costal area, veinlets mostly unbranched, numerous, with fine, stepped cross-veins.

Description. Incomplete forewing. Probably slightly shrunken on preservation since all longitudinal veins are raised slightly. Very broad costal area with close, parallel, apparently

unbranched veinlets. Cross-veins present, slightly stepped, on these veinlets. Many of the branches from the Rs divide close to their point of origin, producing rows of parallel veins to the wing margin. Anal area not preserved.

HOLOTYPE. I.3968, Durdlestone Bay, Dorset: Brodie colln, 1898. Lower Cretaceous (Durlston formation). Dimensions: 12 mm (estimated wing length, 14 mm).

DISCUSSION. The specimen is preserved on a small piece of rock with several other insect fossils.



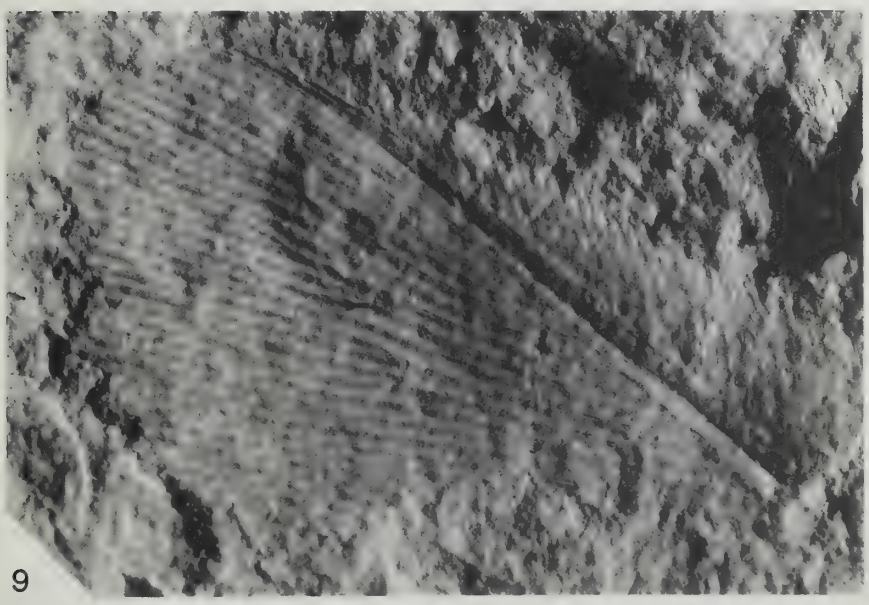


Fig. 8 *Actinophlebia intermixta* (Scudder). Holotype, I.3577. Upper Lias, Gloucestershire (11 mm).
Fig. 9 *Pterinoblattina pluma* (Giebel). Holotype, I.3968. Lower Cretaceous, Dorset (12 mm).

P. pluma differs from *Actinophlebia* in the extensive branching of the radial sector branches close to their point of origin. The large costal area has apparently unbranched veinlets on which there are some cross-veins.

Pterinoblattina penna Scudder 1885
Fig. 10

1885 *Pterinoblattina penna* Scudder: Scudder: 106 (Blattodea).
1886 *Pterinoblattina penna* Scudder: 470; pl. 48, fig. 14.
1890 *Pterinoblattina penna* Scudder: 361; pl. 22, fig. 14.
1906 *Pterinoblattina penna* Scudder; Handlirsch: 608 (Neuroptera).

DIAGNOSIS (from illustration). Large costal area with branched veins. Sc and R close (it is difficult to see in the illustration if they join); Scudder wrote that they 'approach each other very gradually'. Rs has about 18 branches.

HOLOTYPE. I.12324, Durdlestone Bay, Dorset; Brodie colln (specimen not traced). Purbeck. Dimensions: 13 mm × 9 mm, estimated wing length 15 mm.

DISCUSSION. This species is retained in the genus *Pterinoblattina* pending examination of the holotype. There are, however, some basic differences between Scudder's figure of *P. penna* and *P. pluma*; for example, the figure shows many more branches on the radial sector vein and that the costal veinlets are clearly branched.

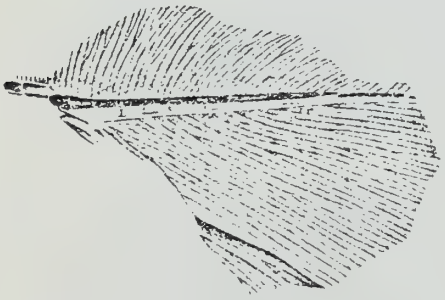


Fig. 10 *Pterinoblattina penna* Scudder. Venation, from Scudder, 1886: fig. 14.

Family **KALLIGRAMMATIDAE** Handlirsch, 1906

This is a group of large (wingspan 80–200 mm) neuropterous insects in which the hind wing is narrower than the much-enlarged forewing. The costal area is twice as wide as the subcostal and radial areas together. Cross-veins are usually numerous and a large eye-spot is often present on the forewing. Apical branches of MA form rows in front of MP, running to the outer (terminal) margin.

Genus ***PARACTINOPHLEBIA*** Handlirsch, 1906

1906 *Paractinophlebia* Handlirsch: 477.

TYPE SPECIES. *Pterinoblattina curtisii* Scudder, 1886, by monotypy.

DISCUSSION. This genus was proposed by Handlirsch for an incomplete forewing, described by Scudder as a cockroach. There is insufficient preserved to decide on its affinities within the Neuroptera and it is only transferred provisionally to the Kalligrammatidae on grounds of size and arrangement of the few preserved veins. No significant definition of this monotypic genus, based on the single incomplete specimen, can be given.

Paractinophlebia curtisii (Scudder 1886)
Fig. 12

1886 *Pterinoblattina curtisii* Scudder: 471; table 48, fig. 16.
1890 *Pterinoblattina curtisii* Scudder: 363; pl. 22, fig. 16.
1906 *Paractinophlebia curtisii* (Scudder); Handlirsch: 477.
1939 *Paractinophlebia curtisii* (Scudder); Handlirsch: pl. 6, fig. 115.

DESCRIPTION. (Wing too incomplete for diagnosis). Forewing, small apical part of R and Sc preserved, running close together. All radial veins branch near wing margin, actual margin not preserved. Rs with many parallel veins, cross-veins numerous.

HOLOTYPE. I.3585, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. Dimensions: Wing 25 mm × 13 mm, incomplete, estimated wing length 35–40 mm.

DISCUSSION. This is placed in the Kalligrammatidae because of its size and the numerous parallel veins with cross-veins. These are regarded as diagnostic and are used to separate the Kalligrammatidae from the Psychopsidae. It differs from *Megapolystoechus* Tillyard in the main longitudinal veins which run more towards the outer (terminal) margin rather than the posterior margin as they do in *Megapolystoechus*.

Family **PROHEMEROBIIDAE** Handlirsch, 1906

Although Tillyard suggested that this family was characterized by a large number of branches on the radial sector ('immense development of parallel branches', Tillyard, 1933: 11) this does not fit the original concept proposed by Handlirsch (1906). Tillyard placed genera in Prohemerobiidae where there were 20–27 branches on the radial sector, whereas in Handlirsch's original description, and his later usage in 1939, only species with 7–11 branches on the radial sector were included. Martynova (1962) recognized this and removed the genera placed by Tillyard (1933) in Prohemerobiidae. The original definition proposed by Handlirsch is used here with slight modification.

Genus ***PROHEMEROBIUS*** Handlirsch, 1906

1906 *Prohemerobius* Handlirsch: 474.

TYPE SPECIES. *Prohemerobius dilaroides* Handlirsch, here designated. Upper Lias. Germany.

DIAGNOSIS. Forewing rounded, not triangular in outline. Sc free from R, reaching nearly to apex of wing. R branched near apex. Rs with 6–10 parallel branches. Branches of Rs divide near wing margin; posterior branches of Rs sometimes with forks one-third from wing margin. M close to (? joins) R. MP usually forked. Cu divided, often with long CuP. Anal veins roughly parallel, curve towards wing margin. Jurassic, Europe.

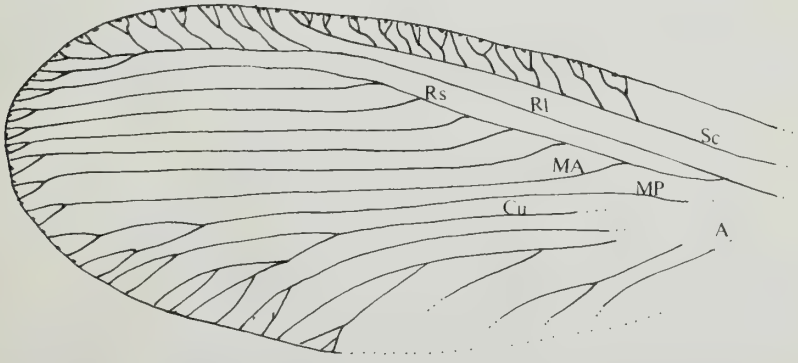
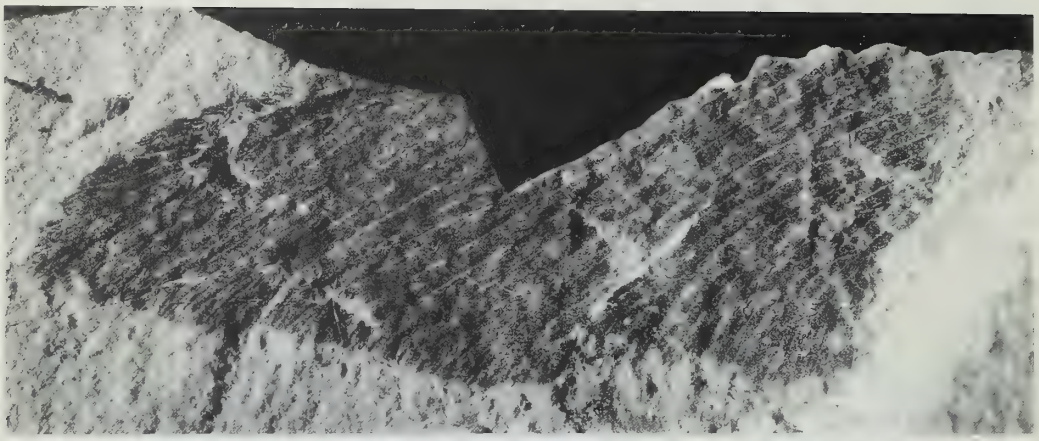


Fig. 11 *Prohemerobius aldertonensis* sp. nov. Venation. A—Anal, Cu—Cubital, MA—Anterior medial, MP—Post medial, Sc—Subcostal, R1—First radial, Rs—Radial sector.



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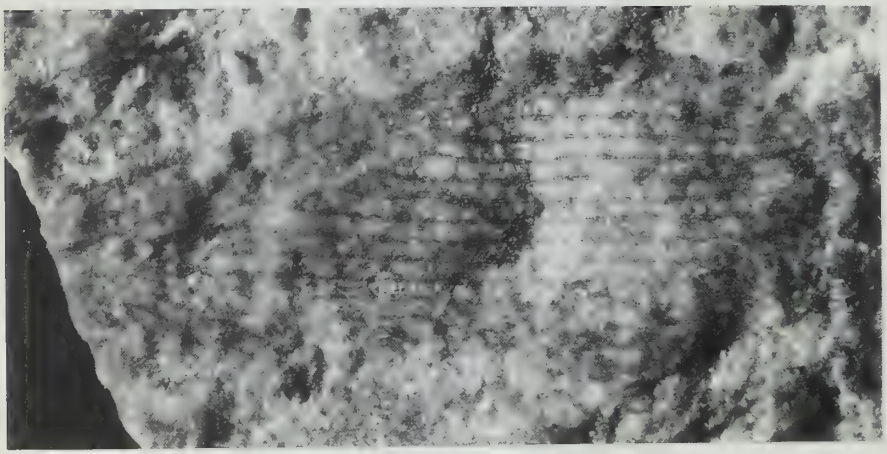

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Fig. 12 *Paractinophlebia curtisii* (Scudder). Holotype, I.3585. Upper Lias, Gloucestershire (25 mm).
Fig. 13 *Prohemerobius aldertonensis* sp. nov. **Holotype**, I.11304. Upper Lias, Gloucestershire (4.7 mm).

Discussion. The Permian family Palaemerobiidae also includes rather small species (Martynova 1962) but in these both the cross-veins from many cells in the wings and branches from the radial sector are usually themselves branched at, or near, the middle of the wing.

Prohemerobius aldertonensis sp. nov.
Figs 11, 13

Diagnosis. As genus but with radial veins reaching nearly to apex of wing.

Name. Locality Alderton, Gloucestershire.

Description. Forewing with radial area wider than subcostal, both together about equal to width of costal area. The base of the wing is damaged; seven, possibly eight, Rs branches. M branched, possibly with short unbranched second cubital. Anal veins obscured. Trichosors present.

HOLOTYPE. I.11304, Alderton, Gloucestershire; Brodie colln, 1898. Upper Lias. Dimensions: 4·7 mm × 1·9 mm.

DISCUSSION. This species has fewer branches on the radial sector than the species of *Prohemerobius* described by Handlirsch (1906, 1939) or Bode (1953) from the Upper Lias of Germany; otherwise the venation is broadly similar.

Family **PSYCHOPSIDAE** Handlirsch, 1906

A single forewing of a psychopsid has been identified in a collection of Wealden (Lower Cretaceous) insects (Jarzembowski 1984: fig. 31).

MATERIAL. In.64632, Clockhouse Pit, near Dorking, Surrey. Weald Clay. Dimensions: wing 32 mm.

Order **RAPHIDIOPTERA**, snakeflies

Two specimens were found in the Lower Lias of Dorset (Whalley 1985) and one from the Lower Cretaceous of Surrey (Jarzembowski 1984: fig. 30).

Family **MESORAPHIDIIDAE** Martynov, 1925

Genus ***MESORAPHIDIA*** Martynov, 1925

Mesoraphidia sp.

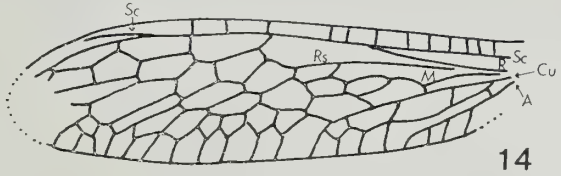
1984 Mesoraphididae Jarzembowski: 82; fig. 30 (unnamed).

MATERIAL. In.64633, near Dorking, Surrey. Lower Cretaceous. Dimensions: wing 11 mm.

Mesoraphidia confusa (Whalley 1985)
Figs 15, 16

1985 *Metaraphidia confusa* Whalley: 148; figs 44, 45.

HOLOTYPE. GSM 117552, Charmouth, Dorset; in British Geological Survey colln. Lower Jurassic. Dimensions: wing 14·5 × 4·8 mm.



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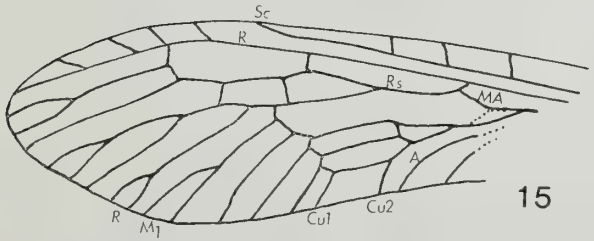

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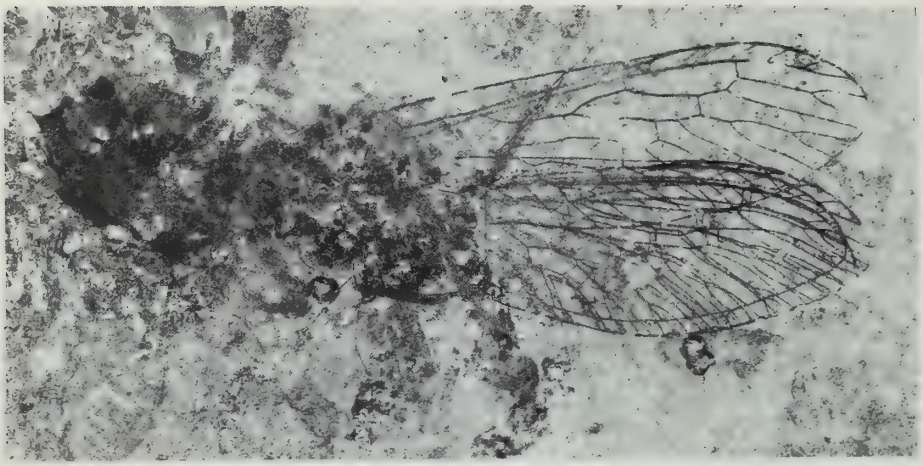
Fig. 14 *Priscaenigma obtusa* Whalley. Venation.
Fig. 15 *Metaraphidia confusa* Whalley. Venation.



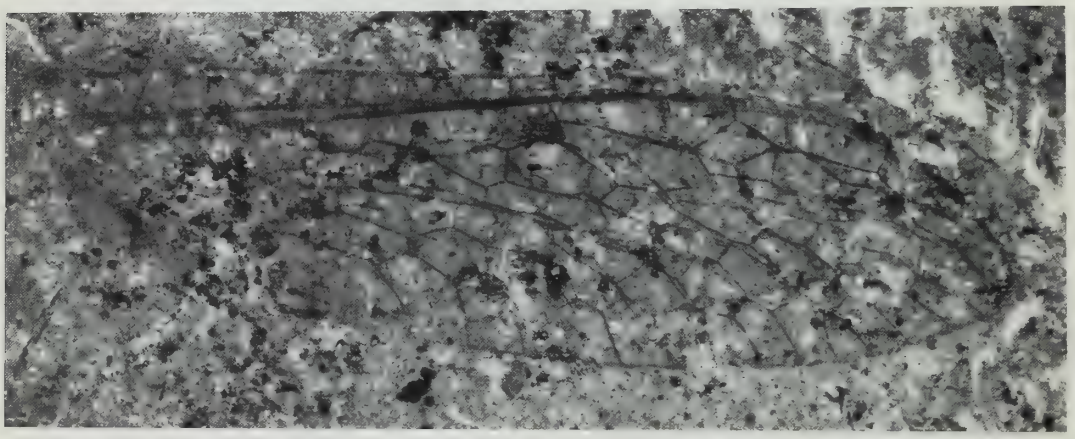


Fig. 16 *Metaraphidia confusa* Whalley. Holotype, GSM 117552. Lower Lias, Dorset (14·5 mm), in British Geological Survey colln.
Fig. 17 *Priscaenigma obtusa* Whalley. Holotype, I.53898. Lower Lias, Dorset (12·6 mm).

Family **BAISSOPTERIDAE** Martynova, 1961

Genus ***PRISCAENIGMA*** Whalley, 1985

Priscaenigma obtusa Whalley 1985
Figs 14, 17

1985 *Priscaenigma obtusa* Whalley: 148; figs 43, 46.

HOLOTYPE. In.53898, Black Ven, Charmouth, Dorset. Lower Jurassic. Dimensions: wing 12·6 mm.

DISCUSSION. Some doubt was expressed in the original description of the correct family for this species. It differs from the type of Baissopteridae in the number of cells in the median area and has longer subcostal veins and a longer radial cell. Since no further material is available the species is retained in the Baissopteridae.

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